BULLETIN

OF

ENTOMOLOGICAL RESEARCH.

ISSUED BY THE COMMONWEALTH
INSTITUTE OF ENTOMOLOGY

EDITOR : THE DIRECTOR

VOL. 45.

LONDON :

COMMONWEALTH INSTITUTE OF ENTOMOLOGY,
56, QUEEN'S GATE, S.W.7.
1955.

A

Commonwealth Agricultural Bureaux.

Executive Council.

W. F. C. Morton, *Chairman*, Union of South Africa.

J. E. C. Coventry, B.A., M.Sc., *Vice-Chairman*, Federation of Rhodesia and Nyasaland.

W. C. Tame, United Kingdom.

Lieutenant-Colonel J. G. Robertson, B.S.A., F.R.S.A., Canada.

W. Ives, M.Ec., Australia.

V. Armstrong, B.Sc., Ph.D., D.I.C., New Zealand.

P. N. Haksar, Counsellor (External Department) of the High Commissioner for India in the United Kingdom, India.

A. M. Chowdhury, Pakistan.

A. I. Perera, C.B.E. (for H. E. the High Commissioner for Ceylon), Ceylon.

C. E. Lambert, C.M.G., Colonial Territories.

Sir Herbert Howard, *Secretary*, Farnham House, Farnham Royal, nr. Slough, Bucks.

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

Director and Editor.

W. J. Hall, C.M.G., M.C., D.Sc.

Assistant Director.

E. O. Pearson, B.A.

Head Office—c/o British Museum (Natural History), Cromwell Road, London, S.W.7.

Publication Office and Library—56, Queen's Gate, London, S.W.7.

CONTENTS.

PAGE

AITKEN, T. H. G.
The Culicidae of Sardinia and Corsica (Diptera) (*illustrated*) .. 437

ASAHINA, E., AOKI, K. & SHINOZAKI, J.
The Freezing Process of Frost-hardy Caterpillars (*illustrated*) .. 329

BANKS, C. J.
A Method for estimating Populations and counting large Numbers of *Aphis fabae* Scop. (*illustrated*) 751

BARNES, H. F.
Gall-midge Larvae as Endoparasites, including the Description of a Species parasitising Aphids in Trinidad, B.W.I. 769

BROWN, A. W. A.
Studies on the Responses of the Female *Aëdes* Mosquito. Part VI.—The Attractiveness of coloured Cloths to Canadian Species .. 67

BROWN, E. S.
The Biology of the Coconut Pest *Melittomma insulare* (Col., Lymexylonidae), and its Control in the Seychelles (*illustrated*) 1

BROWN, E. S.
Xyleborus morstatti Hag. (Coleoptera, Scolytidae), a Shothole Borer attacking Avocado Pear in the Seychelles 707

BURNETT, G. F.
The Effect of Poison Bait Cattle on Populations of *Glossina morsitans* Westw. and *G. swynnertoni* Aust. (*illustrated*) 411

CHARLES, L. J.
Toxicity of the Botanical Insecticide *Ryania speciosa* to *Culex pipiens fatigans* Wied. 403

DAVEY, P. M.
Quantities of Food eaten by the Desert Locust *Schistocerca gregaria* (Forsk.) in Relation to Growth (*illustrated*) 539

DAVID, W. A. L. & GARDINER, B. O. C.
The Action of the Systemic Insecticide Systox, on Aphids .. 683

DAVID, W. A. L. & GARDINER, B. O. C.
The Action of the Systemic Insecticide Systox, on *Pieris brassicae* (L.) and *Phaedon cochleariae* (F.) (*illustrated*) 693

DELUCCHI, V.
Pullus impexus (Muls.) (Coleoptera, Coccinellidae), a Predator of *Adelges piceae* (Ratz.) (Hemiptera, Adelgidae), with notes on its Parasites (*illustrated*) 243

DOBSON, R. M.
The Species of *Carpophilus* Stephens (Col. Nitidulidae) associated with Stored Products (*illustrated*) 389

CONTENTS.

PAGE

GARNHAM, P. C. C. & MCMAHON, J. P.
Final Results of an Experiment on the Control of Onchocerciasis by Eradication of the Vector 175

GEERING, Q. A. & BAILLIE, A. F. H.
The Biology of Red Bollworm, *Diparopsis watersi* (Roths.) in northern Nigeria (*illustrated*) 661

GILLIES, M. T.
Studies in House Leaving and Outside Resting of *Anopheles gambiae* Giles and *Anopheles funestus* Giles in East Africa. I.—The Outside Resting Population (*illustrated*) 361

GILLIES, M. T.
Studies in House Leaving and Outside Resting of *Anopheles gambiae* Giles and *Anopheles funestus* Giles in East Africa. II.—The Exodus from Houses and the House Resting Population (*illustrated*) 375

GLASGOW, J. P.
Glossina palpalis fuscipes Newst. in Lakeside and in Riverine Forest (*illustrated*) 563

HADDOW, A. J.
Studies of the Biting-habits of African Mosquitos. An Appraisal of Methods employed, with special Reference to the twenty-four-hour Catch (*illustrated*) 199

HAUFE, W. O.
The Effect of atmospheric Pressure on the Flight Responses of *Aëdes aegypti* (L.) (*illustrated*) 507

HOCKING, K. S., BURNETT, G. F. & SELL, R. C.
Aircraft Applications of Insecticides in East Africa. VII.—An Experiment against the Tsetse Flies, *Glossina morsitans* Westw. and *G. swynnertoni* Aust., in the Rainy Season (*illustrated*) .. 605

HOCKING, K. S., BURNETT, G. F. & SELL, R. C.
Aircraft Applications of Insecticides in East Africa. VIII.—An Experiment against the Tsetse Fly, *Glossina swynnertoni* Aust., in an isolated Area of Thornbush and Thicket (*illustrated*) .. 613

HOCKING, K. S., YEO, D. & ANSTEY, D. G.
Aircraft Applications of Insecticides in East Africa. VI.—Applications of a coarse Aerosol containing DDT to control the Tsetse Flies, *Glossina morsitans* Westw., *Glossina swynnertoni* Aust. and *Glossina pallidipes* Aust. (*illustrated*) 585

KERR, R. W.
Rearing *Drosophila melanogaster* Mg. for Insecticide Investigations (*illustrated*) 313

KERR, R. W.
A Method for the Topical Application of Small Measured Doses of Insecticide Solutions to Individual Insects (*illustrated*) .. 317

KERR, R. W.
Variation with Age in the Susceptibility to DDT and the Respiration Rate of male and female *Drosophila melanogaster* Mg. (*illustrated*) 323

PAGE

KIRKPATRICK, T. W.
Notes on *Pseudendaphis maculans* Barnes, a Cecidomyid Endoparasite of Aphids in Trinidad, B.W.I. (*illustrated*) 777

LAIRD, M.
Anopheles and Malaria at Aneityum, New Hebrides 279

LAIRD, M.
A Mosquito Survey in New Caledonia and the Belep Islands, with new Locality Records for two Species of *Culex* (*illustrated*) .. 285

LAIRD, M.
The Mosquitos of Aitutaki, southern Cook Islands (*illustrated*) .. 423

LE PELLEY, R. & KOCKUM, S.
Experiments in the Use of Insecticides for the Protection of Grain in Storage (*illustrated*) 295

LEWIS, C. T.
Studies concerning the Uptake of Contact Insecticides. I.—The Anatomy of the Tarsi of certain Diptera of Medical Importance (*illustrated*) 711

LEWIS, D. J.
Muscidae of Medical Interest in the Anglo-Egyptian Sudan (*illustrated*) 783

MCINTOSH, A. H.
Temperature Coefficients of Insect Kill by volatile solid Insecticides 137

MAQSUD NASIR, M.
Responses of Pests to Fumigation. V.—The Toxicity of the free and sorbed Vapours of BHC and DDT to some Insects infesting Stored Products 639

MILLER, N. C. E.
Two new Species of Miridae (Hemiptera-Heteroptera) (*illustrated*) 703

NARAYANAN, E. S. & CHAUDHURI, R. P.
Studies on *Stenobracon deesae* (Cam.), a Parasite of certain Lepidopterous Borers of graminaceous Crops in India (*illustrated*) .. 647

NIELSEN, E. T. & HAEGER, J. S.
Pupation and Emergence in *Aëdes taeniorhynchus* (Wied.) (*illustrated*) 757

PARSONS, B. T.
Field Observations on a Breeding Place of *Glossina pallidipes* Austen in Kenya (*illustrated*) 163

POLLARD, D. G.
The Melon Stem-borer, *Apomecyna binubila* Pascoe (Coleoptera: Lamiinae) in the Sudan (*illustrated*) 553

SIMMONDS, F. J.
Host Finding and Selection by *Spalangia drosophilae* Ashm. (*illustrated*) 527

CONTENTS.

PAGE

Squire, F. A.
Observations on the Incidence of Trypanosomes in *Glossina palpalis* (R.–D.) in Sierra Leone (*illustrated*) 797

Swirski, E.
Fruit Tree Aphids of Israel (*illustrated*) 623

Tait, E. M.
Some Notes on the Life-history and Habits of *Theraptus* sp. (Coreidae) 429

Tait, E. M.
Some Experiments in Cross-breeding of the Coreid Bug, *Theraptus* sp. 433

Talhouk, A. S.
Further Trials with Parathion Dusts against *Eurygaster integriceps* Put. (Hemiptera, Pentatomidae) (*illustrated*) 495

Van den Berghe, L. & Lambrecht, F. L.
Notes on the Discovery and Biology of *Glossina brevipalpis* Newst. in the Mosso Region (Urundi) (*illustrated*) 501

Way, M. J.
Studies of the Life History and Ecology of the Ant *Oecophylla longinoda* (Latreille) (*illustrated*) 93

Way, M. J.
Studies on the Association of the Ant *Oecophylla longinoda* (Latr.) (Formicidae) with the Scale Insect *Saissetia zanzibarensis* Williams (Coccidae) (*illustrated*) 113

Williams, G.
Field Observations on the Cacao Mirids, *Sahlbergella singularis* Hagl. and *Distantiella theobroma* (Dist.), in the Gold Coast. Part III. Population Fluctuations (*illustrated*) 723

Williams, G. C.
Observations on the Life History of *Laemophloeus minutus* (Ol.) (Col. Cucujidae) when bred on various Stored Cereals and Cereal Products 341

Williams, G. C.
Obervations on the Effect of Exposure to a Low Temperature on *Laemophloeus minutus* (Ol.) (Col. Cucujidae) 351

Wilson, S. G.
A Preliminary Study of the *Glossina pallidipes* Austen Population at Makueni, Kenya (*illustrated*) 141

Woodroffe, G. E.
An additional Note on the Fauna of Birds' Nests in Britain .. 135

Woodroffe, G. E. & Southgate, B. J.
An Investigation of the Distribution and Field Habits of the Varied Carpet Beetle, *Anthrenus verbasci* (L.) (Col. Dermestidae) in Britain, with comparative Notes on *A. fuscus* Ol. and *A. museorum* (L.) (*illustrated*) 575

PAGE

WOOTTEN, N. W. & SAWYER, K. F.
The Pick-up of Spray Droplets by flying Locusts (*illustrated*) .. 177

YEO, D.
Aircraft Applications of Insecticides in East Africa. IX.—Further Experiments on the Deposition in open Country of a coarse Aerosol released from an Aircraft (*illustrated*) 745

YEO, D. & THOMPSON, B. W.
Aircraft Applications of Insecticides in East Africa. V.—The Deposition in open Country of a coarse Aerosol released from an Aircraft (*illustrated*) 79

DATES OF PUBLICATION IN PARTS

Part I	pp. 1–242	..	31 March 1954
Part II	pp. 243–410	..	28 June 1954
Part III	pp. 411–646	..	27 September 1954
Part IV	pp. 647–801	..	30 December 1954

ERRATA.

Page 370, line 13, delete " *theileri* "

Page 402, column 2, line 13, for " *Lonchorcarpus* " read " *Lonchocarpus* "

Page 456, 8 lines from end, delete sentence beginning " In addition, another character . . . "

Page 477, 7 lines from end, for " (Edwards & Et. Sergent) " read " (Edm. & Et. Sergent) "

Page 621, line 12, for " unseasonal " read " unseasonable "

Page 711, 14 lines from end, for " (R.D.) " read " R.D."

Page 721, lines 28–29, for " *Phormia* (*Protophormia*) *terraenovae* (R.D.) " read " *Phormia* (*Protophormia*) *terraenovae* R.D."

Page 769, 17 lines from end, for " larvae " read " larva "

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

BULLETIN
OF
ENTOMOLOGICAL RESEARCH.

Vol. 45. 1954.

THE BIOLOGY OF THE COCONUT PEST *MELITTOMMA INSULARE* (COL., LYMEXYLONIDAE), AND ITS CONTROL IN THE SEYCHELLES.

E.M.N.

By E. S. Brown.

Commonwealth Institute of Entomology.

(Plates I–VI.)

Contents.

PAGE
Introduction ... 1
Life-History and Biology ... 3
Feeding Habits of the Larva and associated Micro-organisms ... 10
Development of Infestations in individual Palms ... 18
The Progress of Infestations in a Plantation ... 23
Symptoms of Attack ... 24
Occurrence in native Palms ... 27
Geographical Distribution, Origin and History ... 28
Ecological Factors in Distribution ... 31
Associated Organisms ... 42
Control Measures ... 45
Summary ... 62
Acknowledgements ... 63
References ... 64

Introduction.

The Lymexylonid genus *Melittomma* was separated off from *Hylecoetus* Latr. by Murray (1867), for the reception of *H. brasiliensis* Castelnau (designated as the genotype) and a species which he thought was new and described as *M. castaneum*, but which had in fact already been described earlier as *Hylecoetus africanus* J. Thoms. *Melittomma insulare* was first described by Fairmaire (1893) from the Seychelles, his description being of the adult stage only.

The "petit moutouc", as the larva of *M. insulare* was called locally, was first recognised by the Government of Seychelles as a pest of coconuts about

1903, although the first description of it, by Gahan, did not appear until 1908. Later there were frequent references to it, and to earlier methods of combating it, by Dupont and others (Hibbs, 1922; Lyne, 1923; Squibbs, 1934) in the annual reports of the Department of Agriculture. In Madagascar, the only other country from which the species is known, it was first recorded in 1911 (Herscher & Millot) and known as "la maladie"; its ravages are referred to by Estève (1925), and a more detailed account of the earlier recorded history has recently been given by Frappa (1948), where further references will be found. In the last few decades there have been several accounts and references in the literature, most of which are given in the bibliography. Among the most recent are those of Lepesme (1947) and Evans (1952); it should be stated that the adult insect figured by Lepesme on p. 501 is certainly not *Melittomma insulare*, but is a species of the genus *Atractocerus*, possibly *A. brevicornis* (L.).

21 340

The first detailed study of the biology and life-history of the insect was made by Vesey-FitzGerald (1941), who regarded it as a pest of sufficient importance to merit serious attention. Frappa's later work (*loc. cit.*) takes us over much the same ground, with some additional information relating especially to Madagascar. Vesey-FitzGerald made some recommendations for control measures, based largely on a selection of the best of those which had for some years been practised by planters. These recommendations were unfortunately not widely followed, with the result that in certain areas, notably the island of Praslin, the pest has recently become of such importance as to threaten to make coconut cultivation unremunerative, and to induce the Seychelles Government to institute a large-scale investigation of control methods from all angles. Some idea of the course of recent developments may be gained from recent reports of the Department of Agriculture (Nichols, 1945; Pound, 1946–7; Milsum, 1949–50; Durocher Yvon, 1949–52).

Accordingly, in February 1952, a team of three entomologists arrived in Seychelles: Dr. F. J. Simmonds to study the problem from the biological control aspect; Mr. D. Vesey-FitzGerald principally to study the ecological aspect and the status of the pest as compared with what he had found in his earlier work; and the writer to investigate the problem generally, with special reference to the possibility of insecticide control. Dr. Simmonds remained a few weeks to study the insect in its natural environment before leaving in search of possible parasites elsewhere, (his report on the biological control aspect is to be published separately). Mr. Vesey-FitzGerald remained for three months, and his assistance by virtue of his previous experience of *Melittomma* and of the islands generally was of inestimable value. The writer remained in the islands until March 1953, being latterly almost entirely concerned with insecticide experiments. A short visit was made to Madagascar in November–December 1952, to enable a study of the insect to be made there; only three weeks were spent on the island.

As the result of a survey of plantations made before he left, Mr. Vesey-FitzGerald did not form the conclusion that the incidence of *Melittomma*, as expressed by the percentage of palms infested in samples, had increased significantly since his previous visit twelve years before (Brown, 1953). In fact, such figures as we had available before he left, showed, if anything, the contrary (Table I). This, however, does not mean that the beetle is not a serious pest deserving careful attention and any reasonable expenditure which its reduction may necessitate. One has only to see parts of the islands of Praslin or Thérèse, where the attack has undoubtedly become very much more serious in recent years, and compare the former with the neighbouring island of La Digue, which is free from the pest, in order to form an opinion of the serious effect its depredations may have at their worst. Few of the samples in Table I are from Praslin; if there were more it might tell a different story.

A few examples of the extent of the damage which has been known to result

TABLE I.

Comparison of the percentage of palms attacked by *Melittomma* in samples taken in 1939 and 1952.

Percentage of palms attacked by *Melittomma*	0%	1–25%	26–50%	51–75%	76–100%
1939 . . . . (42 samples)	4 9·5%	2 4·7%	8 18·0%	14 33·3%	14 33·3%
1952 . . . . (39 samples)	3 7·7%	11 28·2%	4 10·2%	11 28·2%	10 25·6%

from acute attacks in parts of Praslin may be quoted. One estate was taken over in 1927, when it produced 300 nuts per month, being at that time largely planted with other crops; coconuts were then planted extensively, and increase in production started in 1935–36, rising to 22,000 nuts per month by 1948. Meanwhile heavy attack by *Melittomma* had developed, bringing about a rapid fall in production, which in 1952 was only 15,000 nuts per month. The decrease is attributable to palms falling in their prime, due to the rotting of the base of the trunk resulting from attack. In another area of 42 acres 25 palms fell within a week, most of them on one day when the breeze was strong; all of them had rotted centres to the trunk-bases. In another estate of 350 acres palms have recently been falling at the rate of about 150 a year; the appearance of this plantation (Pl. V, fig. 6) at the time of writing is alone enough to convince one of the potential danger to coconut cultivation.

Life-History and Biology.

There is not a great deal to add to the general outline of the life-history, from the present investigation, to what has already been contributed by Vesey-FitzGerald (1941). *Melittomma* is notoriously difficult to rear from egg to adult, and no serious attempt has been made, since the life-cycle is long. Some additional information has been obtained about the various stages, however, and this will now be given (under separate headings).

Eggs and oviposition.

It is not always easy to persuade a female to oviposit in captivity. Freshly emerged females have been frequently kept in tins or boxes with males present, and provided with wood-chips or coconut bark, with or without soil; they have only occasionally laid eggs, even although coition has taken place and subsequent dissection has revealed fully-developed eggs in the abdomen. The most successful method has been to place a female in a tin, fitted with a gauze window and clamped on to the trunk of a palm in an encircling ring of banding grease to keep ants away; soil or wood-chips may be included in the tin. In such conditions the female usually hides in any available crevices, and is frequently seen extruding her ovipositor and making exploratory movements with it, inserting it into little crevices in the bark or between adventitious roots. The tip of the ovipositor (fig. 1) is provided with a pair of small appendages which are probably sensory in function, and adapted for exploring and detecting suitable crevices for oviposition. Occasionally after such behaviour subsequent examination showed that eggs had been laid.

Although the eggs may sometimes be laid away from the trunk, as suggested by Vesey-FitzGerald, there is little doubt that the base of the trunk is the normal site. The habit of the adult beetle of hiding in small crevices (Pl. I, fig. 1), often in frenzied haste, appears to be a thigmotactic response, and automatically takes it to the places which are most favourable for oviposition, such as the spaces between closely-packed adventitious roots on the base of the trunk, or wounds in the bark.

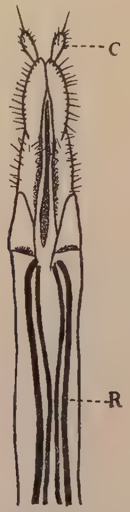


Fig. 1.—Ovipositor of female *Melittomma insulare* from Seychelles, exserted and cleared to show chitinous supporting rods (R) by transparency. Note the pair of cerci (sensory appendages) at the tip (C).

On the infrequent occasions when oviposition occurs in captivity, the eggs are laid in batches of anything up to 100 or more, as has been stated by other authors; although in the natural state no such batches have ever been found, there is evidence that the same thing occurs (p. 18). The number of eggs contained by individual females is very variable according to the size of the insect, and counts of 18 and 384 are recorded by Vesey-FitzGerald. Eight females which I have dissected contained 84, 88, 186, 210, 324, 346, 364 and 426 eggs, giving an average of 253·5. It will be apparent later (pp. 22–23) that the potential damage which one female may cause is considerable, for 400 odd larvae can do permanent damage to two palms. To judge from the average number of larvae found in individual palms, a female does not usually lay all her eggs on one palm, although without more knowledge of larval mortality one cannot be sure of this.

The egg is sausage-shaped (fig. 2). Vesey-FitzGerald gives the dimensions as 1·0 mm. long and 0·25 mm. wide; I have found them rather larger—18 eggs averaged 1·28 mm. in length and 0·38 mm. in width.

The larva (Pl. I).

The larva has naturally received much attention since it is the stage which does the damage, by boring into the trunk and causing the wood to rot. Descriptions have been given by Gahan (1908) and Vuillet (1913). The larvae of only two other species of the genus have so far been described. These are *M. albitarsis* Blair and *M. sericeum* (Harris); the larvae referred to by Lacordaire (1830) as "*Hylecoetus brasiliensis* Dej. n. sp." were probably not the same as *Melittomma brasiliense* (Cast.), but belonged to another genus. Larvae of *M. albitarsis* were bred from the wood of *Bombax malabaricum* D.C. (Gardner, 1937; Beeson, 1941). The larva of *M. sericeum* was first figured by Riley (1874) as " an unknown Tenebrionid " larva, but correctly identified after breeding it from chestnut wood by Hopkins (1894); it has also been figured by Böving and Craighead (1931). In structure the larvae of all three species are very similar. The most remarkable feature is the " tail-piece " at the posterior end, a hoof-shaped, heavily chitinised structure with the posterior face concave and studded with about 17–21 (usually 18) pits (Pl. I, fig. 3); these are of unknown function; in later instars each has a raised rim. The exact number and arrangement of the pits varies from one larva to another, but is constant in successive instars of the same larva (fig. 3). The tail-piece as a whole is used as a ram to push the

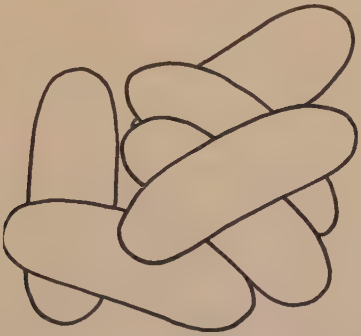


Fig. 2.—Group of eggs of *M. insulare* (× 30).

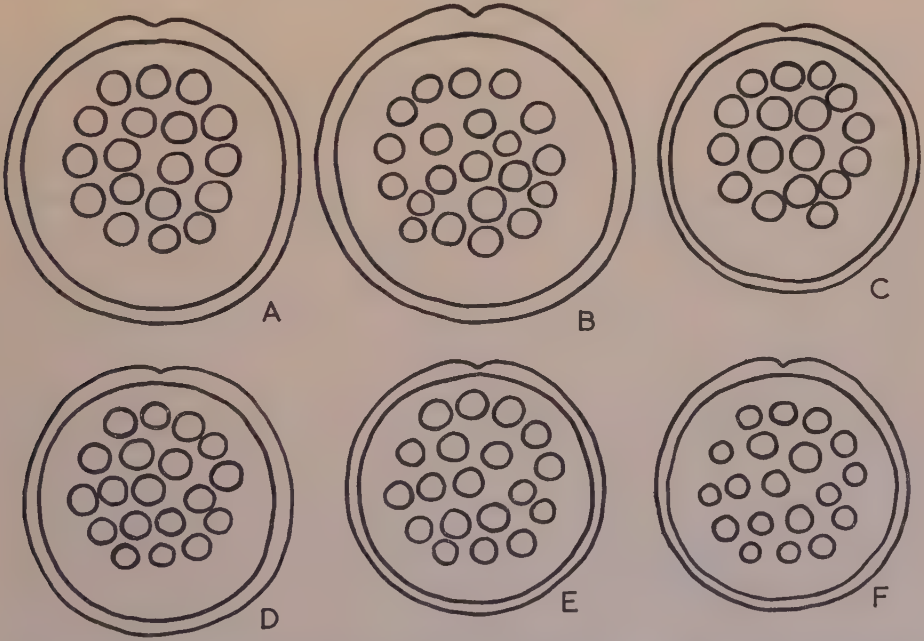


Fig. 3.—Diagrams of rear view of " tail-piece " of larvae of *M. insulare* from Seychelles, showing the arrangement of pits. A–C, three different larvae, showing variation in number and arrangement of pits; D–F, the first, fourth and seventh in a series of exuviae shed by the same larva (see p. 6), showing constant number and arrangement of pits (× 12).

borings towards the mouth of the tunnel, where they appear as small pellets resembling sawdust (Pl. I, fig. 4). The larva thus makes periodic descents, hind end foremost, to the mouth of the tunnel, where its tail-piece can often be seen protruding. After ecdysis, the cast skin also is pushed down the tunnel, the hard tail-piece alone retaining its shape, and is evacuated to the outside together with the wood-borings.

Investigation of the biology and length of life of the larva is to a large extent hampered by the difficulty of rearing it. One cannot observe it in its natural environment, but a certain amount can be done by imprisoning larvae in cells cut in blocks of wood which have been split down the centre (fig. 4), the two halves being tied together with string. The block can be opened daily to watch progress. A larva will live for some time under these conditions, provided the wood is frequently changed before it becomes too dry, which can be delayed by keeping it in a tin; one was kept alive for 3½ months, from 22nd August to 6th December. During this time seven ecdyses took place in 96 days, giving an average of 16 days for each instar. It then pupated, and the adult beetle emerged 11 days later on 17th December. It is curious that this larva was already apparently full-grown at the start, for it did not increase in size; in fact, the size as measured by the width of the cast tail-pieces decreased towards the end, the figures for successive ecdyses being in the ratio 74, 73, 74, 73, 69, 68, 64. No other larva was successfully kept as long as this, but several were kept through two or three instars, and the duration of an instar always averaged about 16 days. Even smaller larvae (about half-developed) showed very little increase in size in successive instars, and it is evident that the larval state may extend over a very long time. Although it is true that the development and growth may have been slowed down on account of artificial conditions, it is probably not much faster in nature under certain circumstances, such as in older palms with dry wood. Very occasionally a series of cast tail-pieces from consecutive ecdyses are found accumulated one above the other at the base of a tunnel, when the larva has for some reason been unable to push the first one out. In one such series of four (Pl. I, fig. 6) there was scarcely any difference in size between them, the most recent being wider than the earliest only in the ratio of 89 : 88.

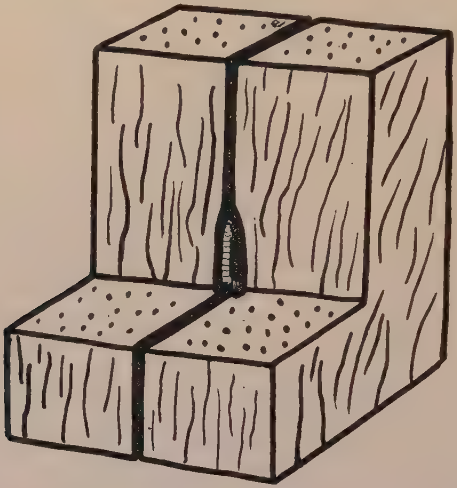


Fig. 4.—Block of coconut wood for rearing larvae; a part of the block has been removed to show the larva in the cell excavated for it in the centre. The two halves of the block are held together with string.

The duration of the larval state was estimated by Vesey-FitzGerald to be about one year, but probably very variable. We can only say as the result of the above observations that it can hardly be less than this, and under unfavourable conditions is probably a great deal more.

The method of movement of larvae up and down the tunnels was investigated by imprisoning them in glass tubes packed with wood, so that they could be observed through the glass. The first thoracic segment can be expanded or contracted, apparently by blood-pressure; so also can a ventral, spinose protuberance on the anal segment (Pl. I, fig. 5). The larva fits its tunnel fairly closely (Pl. I, fig. 7), so that when either the thoracic or the anal segment is distended, the end in question is clamped in position in the tunnel. The larva first distends the anal segment, thus fixing the posterior end, and at the same time elongates its body, so that the front end moves forward; the thoracic segment is then distended, thus fixing the front end, the anal segment is relaxed, and the body contracted so that the free hind end is drawn up towards the front end. The process is then repeated. Backward movement is effected by the same process in reverse.

An investigation of the feeding of the larva forms an important part of the present investigation, and will be dealt with separately (p. 10 *et seq.*). The following section (p. 18 *et seq.*) also covers certain other aspects of larval biology.

The pupa (Pl. I, fig. 8).

The pupa has previously been figured and described by Vuillet (1913).

Shortly before pupation the larva increases the width of the tunnel to form a pupal cell, usually at or near the apex. It then casts a skin behind it, without pushing it down the tunnel, so that the tail-piece remains, hind face downwards, immediately beneath the cell. The larva then turns round in the cell so that its head faces the entrance of the tunnel, and sheds the last larval skin, so that the tail-piece is above the pupa, with its hind face towards the apex of the tunnel; we thus have a pupa with a cast skin above and below it, as illustrated on Plate I, fig. 9; this arrangement has been observed in captivity and in the natural state. The emerging adult will thus face the entrance of the tunnel, but it appears that the pupa normally works its way to the entrance before emergence, doubtless pushing before it the larval tail-piece which confronts it; on several occasions empty pupa-skins have been found hanging from the mouths of the tunnels. It should be noted that the foregoing account differs in several respects from that given by Vesey-FitzGerald, but it is not impossible that there is some variation in the details of the process.

The duration of the pupal stage is short. One adult was reared in captivity after a pupal period of 11 days; in another case pupation occurred between 5th and 7th December, and the adult emerged on 17th December, giving a period of 10–12 days. The duration is therefore possibly a little shorter than the estimate of "rather over a fortnight" given by Vesey-FitzGerald.

The adult.

A description of the adult is unnecessary, but it is illustrated together with other stages on Plate II.

The size is very variable, the length ranging from 7 to 17 mm. The males are usually much smaller, averaging 10–11 mm., while the females average about 14–15 mm. The measurements of a fair sample work out as follows:—

Length in mm. ...	7	8	9	10	11	12	13	14	15	16	17	18
Males	1	1	11	20	20	11	1					
Females			1	1	4	1	3	3	4	8	3	1

These measurements are taken from the front of the head to the tip of the elytra; in females the tip of the abdomen protrudes beyond, but to varying extents according to whether it is full of eggs or not. The females vary much more in size than the males, small ones being probably due to poor feeding conditions. Extreme specimens are shown on Plate II, fig. 4.

Apart from size, in which there is some overlap between the sexes, the males are easily distinguishable from females by the possession of a conspicuous, branched appendage on the maxillary palps (fig. 5; Pl. II, figs. 2, 3), of unknown function but probably sensory; this is characteristic of the family Lymexylonidae. There is also a slight difference in the form of the antennal segments, which have the serrate processes more slender and acuminate in the male (fig. 5, C).

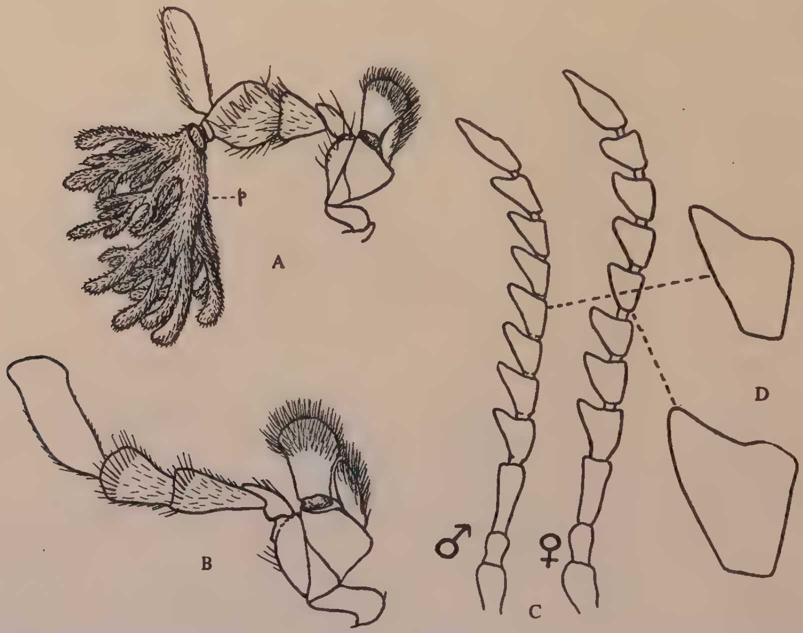


Fig. 5.—A, B, maxillary palps of male and female respectively of *M. insulare* from Seychelles, showing the branched palpal organ in the former (p); C, antennae of male and female from Seychelles; D, 7th antennal segments of each more highly magnified. (A, B, × 30; C, × 15; D, × 50.)

Specimens from Madagascar have been compared carefully with those from the Seychelles, and no difference can be found; this applies to external features, the structure of the palpal organs and aedeagus of the male (fig. 6), and the ovipositor of the female.

The length of life of the adult is very short; in captivity Vesey-FitzGerald found females lived only four days after emergence, and males six days. I have found a rather shorter period, females surviving only 2–3 days as a rule, even when kept in tins or boxes with soil and wood-chips.

In view of the retiring habits and short life, it is not surprising that the adult beetle is known to few planters. It not infrequently comes to light, however, being strictly nocturnal. It seems to fly in the early part of the night, for none have been taken after about 9.30 p.m. although light-traps have occasionally been kept going all night; most have been taken between 7 p.m. and 8.30 p.m.

All our records of adults are summarised in Table II. Those taken at light are recorded separately from those obtained from other sources; the latter were nearly all dissected out of the trunks of palms during examinations of infestations

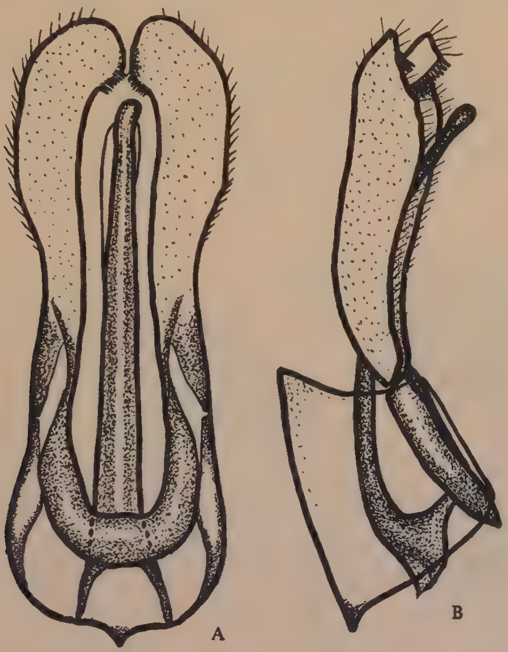


Fig. 6.—Aedeagus of *M. insulare* from Praslin, Seychelles. A, from above; B, from left side (× 50).

TABLE II.

Records of adults in each month during a fourteen-month period in the Seychelles.

Month	Collected at light			Collected from other sources				Grand total
	♂	♀	Total	♂	♀	Sex unknown	Total	
Jan. ..	1	—	1	—	2	34	36	37
Feb. ..	4	1	5	2	3	—	5	10
Mar. ..	6	1	7	6	14	3	23	30
Apr. ..	2	—	2	2	3	—	5	10
May ..	7	—	7	8	6	1	15	22
June ..	—	—	—	7	8	1	16	16
July ..	—	—	—	3	14	—	17	17
Aug. ..	2	—	2	1	9	3	13	15
Sept. ..	1	1	2	2	1	4	7	9
Oct. ..	3	—	3	2	6	—	8	11
Nov. ..	—	1	1	—	1	—	1	2
Dec. ..	—	—	—	1	1	—	2	2
Total ..	26	4	30	34	68	46	148	178

The February and March figures include records of two successive years, 1952 and 1953.

or of insecticide experiments. It is evident that nearly all those which come to light are males, while the majority of those taken in trunks are females. This suggests that the latter tend to remain in the trunk after emergence, the male being of more vagrant habits, but it is also partly due to the small size and greater activity of the males, which enables them to fly more readily and reach the light. In fact, it is commonly thought that the female is virtually incapable of flying any distance; this is not so, however, for although it is nearly always males which are taken at light, I once caught a female flying strongly round an indoor light some six feet from the ground, and fifty yards or more from the nearest palm. On another occasion a female was found at the first floor window of a house, where it had doubtless been attracted by light. A possible important result of this will be discussed on p. 28 *et seq.*

The question of a seasonal life-cycle.

The question of whether the life-cycle is seasonal is important, since it might materially affect the application of control measures. It has been stated to be seasonal by some authors; for instance Herscher and Millot (1911) state that the adult flies in October and November in Madagascar, and Frappa (1948) extends this period as far as January; that is to say, it appears at the beginning of the wet season. This may be so in Madagascar, but it is not so in the Seychelles, where larvae of all stages, and pupae and adults, can be found throughout the year. Since the adult lives only a few days, records of adults obtained give a good idea of whether there is a seasonal emergence period. All adult beetles encountered over a 14-month period in the Seychelles are included in Table II; those taken at light indicate flight, or at least emergence from the trunk, during the months concerned. The numbers obtained from dissection of trunks in different months do not indicate relative frequency, because they depend upon the months in which such work was principally carried out. It is, however, evident that adults are well represented all the year round; the low figures for November and December are due to my absence in Madagascar during most of these two months. It is possible that more adults emerge in the first two or three months of the year, shortly after the heaviest rains have started; this would not be surprising, since the increased sap-flow might enable older larvae to feed up quickly and pupate (see the section on feeding habits, below), and adults would emerge some 10–15 days after pupation.

Pupae tell much the same story. They have been obtained during all the months from January to October; my absence in Madagascar again explains the lack of records in November and December.

Fully-developed eggs have been dissected from females in March, May, June, July and August; they have not been looked for during other months.

It is clear from this evidence that any seasonal incidence in the life-history is no more than a slight tendency at the most, and that control measures carried out at certain times of the year to catch individual stages are not likely to succeed.

Feeding Habits of the Larva, and Associated Micro-Organisms.

Feeding behaviour.

From the habits and habitat of the larva it has apparently been tacitly assumed hitherto to be a genuine wood-feeder, ingesting solid wood and digesting at least some part of it. It was therefore a surprise to find that on dissecting some larvae, no trace of wood whatever was found in the simple, tubular gut (fig. 7), nor even recognisable remains of the soft parenchymatous cells amongst which they normally feed; the only material was a fluid, clear and usually yellowish, but sometimes of a rusty red colour; occasionally a small amount of flocculent matter, without any sign of structure, was found, usually in the hind-gut. Subsequently, nearly fifty larvae were dissected with similar results; they were examined at different times of the day and night, some immediately after removal from the trunk and others after an interval. A batch of some twenty larvae was left in a tube overnight; the next morning no faeces had been passed, and dissection of a number of them revealed only the usual fluid. It thus appeared almost certain that the larva feeds only on the fluid content of the wood, and in order to prove this larvae were kept under artificial conditions which made it possible to examine their manner of feeding under the microcope. Humid, sappy wood was packed into small glass tubes, open at both ends, about 10 cm. long and with a bore of 6 mm. or 8 mm. diameter. A gap was left half

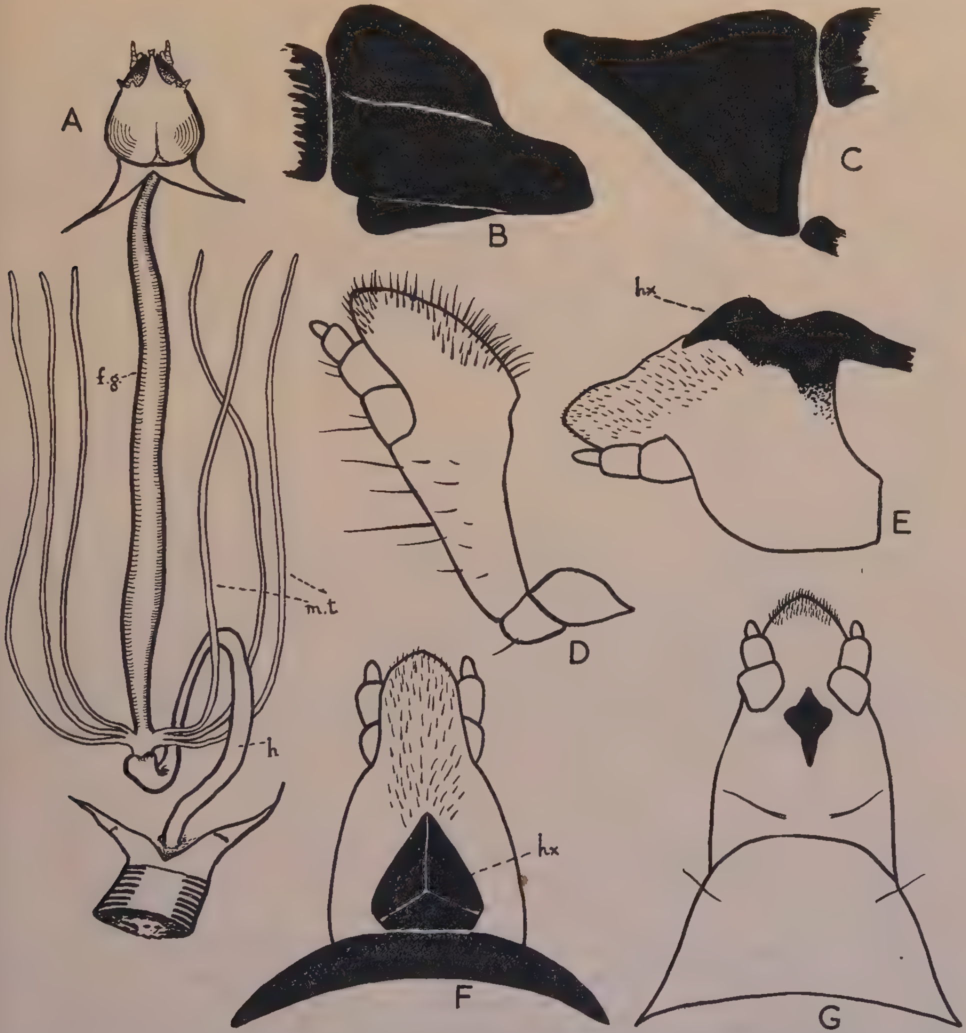


Fig. 7.—Larva of *Melittomma insulare*, gut and mouth-parts: A, gut; *f.g.*, fore- and mid-gut; *h*, hind-gut; *m.t.*, Malpighian tubules: B, C, mandibles (B, left, inner view; C, right, ventral view): D, right maxilla, ventral view. E, F, G, labium, from left side, above, and below respectively; *hx*, hypopharynx.

way up each tube and a larva placed in it. The larvae would then bore into the wood and its behaviour could be observed through the glass. The day after an experiment was set up some of the larvae had bored tunnels; most of the borings had accumulated in the cavities from which they had come, often with a trail passing along the side of the tunnel to the head of the larva, indicating that the material had not passed through the body since they could not have come from the anus. One of the larvae was observed in detail while feeding; it made exploratory movements with the maxillae, and scraped off pieces of the soft, wet parenchyma tissue with the mandibles, or picked up pieces which were already free; it appeared to bite them, as if pressing out the juice. Occasionally it remained still for a few seconds, as if sucking in the fluid extracted with the ligula-like labium (fig. 7): what appeared to be a pumping action of the internal organs could be seen by transparency in the front part of the body. The morsels of wood were then passed back under the body with the mandibles, legs and underside of the head. After a while it withdrew its front end down the tunnel, carrying morsels backwards with its feet. It then repeated the performance, sometimes in the tunnel leading upwards, and sometimes in another which it had excavated downwards from the cavity.

After about half-an-hour's continuous feeding this larva was immediately killed and dissected; the gut was full of clear, slightly yellowish fluid, with no trace of cell structure.

Most larvae appeared to live quite well under these conditions. The wood was kept moist by pipetting on to it drops of fluid, pressed out of moist coconut wood. The larvae did not tunnel much since they could obtain all the fluid they required without; they would sometimes repeatedly work over the morsels of wood previously discarded and which had become recharged with moisture. Some remained in good health for a month, with only one lot of wood but frequent addition of fresh juice. After that the wood was allowed to dry out, and the larvae died within a day or two.

In order to see whether the sap alone suffices for food, larvae were placed in similar tubes, with only a wad of cotton-wool above, and another below each larva to keep it in position (fig. 8). The upper wad of wool was then kept saturated with coconut wood juice; the larvae would feed by sucking fluid out of the cotton-wool in the same way as they do out of wood. Out of ten larvae six were still alive after a fortnight of this treatment, but died immediately after the wool was allowed to dry out.

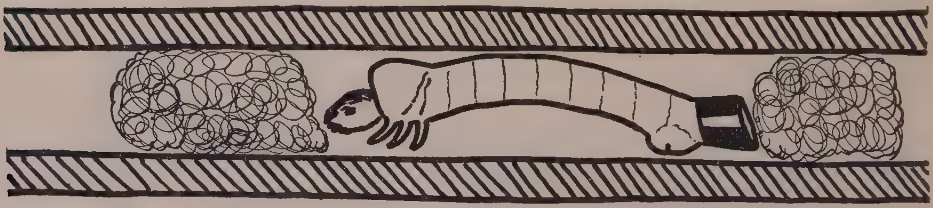


Fig. 8.—Larva of *M. insulare* in glass tube, feeding on fluid extract of coconut wood in cotton-wool

Other experiments on similar lines included the placing of larvae in cotton-wool, and in sawdust of Casuarina wood in glass jars, saturated with coconut wood juice. Many of these died after a few days, apparently due to drowning through having the medium too wet; some, however, lived a week or more. On one occasion a natural infestation was found in a trough-like wound some distance up a trunk, and wood-borings cast out of the tunnels had accumulated in the trough where exudation of sap had converted them into a damp sludge. Several larvae were living in this, and continued to do so for many days when it was placed in a tin. They had evidently emerged from the openings of the tunnels when these had been covered by the accumulated sludge.

There is thus no doubt that the food of the larvae consists principally, if not entirely, of fluid obtained normally direct from the parenchyma tissue. In one trunk which was dissected the wood was abnormally dry from some unknown cause, but otherwise apparently normal; of the few larvae found in it some were moribund and others already dead. The small numbers of larvae normally found in drier trunks may well be due to such mortality. Evidence will later be given from an ecological standpoint that larvae thrive much better in trees where one or more factors tend to produce a high level of humidity in the wood. A knowledge of larval nutrition goes a long way towards explaining this fact.

Associated micro-organisms.

Wood is an unpromising type of food material, and it is not surprising that some insects which depend upon it have evolved more or less complex methods of assimilating it; these depend principally upon association with micro-organisms which are physiologically better equipped for chemical breakdown of the wood into substances simple enough for assimilation by the insects. Many insects wait for normal fungal and bacterial decay to set in, and attack the wood only after it has rotted, and although indirectly dependent upon these organisms there is no simultaneous or close association. Other insects, such as the " ambrosia " beetles, regularly employ fungi which grow on the walls of the tunnels; the fungus is assumed to accumulate nitrogenous foods and the beetles and their larvae eat the fungi; and although in some instances wood is eaten in addition, in others the fungi form their only diet. In other cases there is an endosymbiotic relation, micro-organisms living permanently in the gut of the insect, where they render similar service by pre-digesting the raw food. A useful general survey of the various conditions and degrees of closeness of the relations between insects and micro-organisms is given by Leach (1940).

As far as the present investigation is concerned, it will help to describe first the visible changes which occur in wood infested with the larvae. Around each tunnel there appears a zone of discoloured wood, which was noted by Vesey-FitzGerald who referred to it as " bruised " tissue. In the past it has been attributed to the production of a " caustic liquid " by the larva (Barrett & Mackie, 1912; Copeland, 1931). The colour is usually yellowish-white at first, and a thin, dark brown marginal zone separates it from the surrounding healthy wood (Pl. II, fig. 5). This yellowish wood soon develops a fawn, or sometimes a pinkish or pale rusty-red colour. These colour changes are accompanied by the production of a sweetish, aromatic odour which although somewhat variable is highly characteristic; it suggests a process akin to fermentation, and wood which has undergone this change will be referred to as " fermented " wood. The thickness of the zone round each tunnel is variable, depending upon the rate of spread of fermentation, which in turn depends upon the humidity of the wood. In more humid, sappy wood, where spread is rapid, the zones surrounding adjacent tunnels, if they are not too far apart, coalesce to form a solid block which may extend eventually throughout most of the central portion of the base of the trunk; this amalgamation has already occurred in the wood photographed on Plate II, fig. 5. The fermentation also spreads beyond the tips of the tunnels, in extreme cases passing a foot or more in advance of the larvae. Fermented wood is necrotic and will never recover, but eventually undergoes further changes which are visibly indistinguishable from ordinary rotting. As we pass back from the tip towards the opening of the tunnel the wood becomes darker (Pl. II, fig. 6); it may pass through a bright rusty-red colour but eventually becomes light brown, then dark brown and finally almost black.

A close watch was kept on infested wood for fungi at first, this appearing the most likely type of organism to be associated, but in no case has fresh fermented wood been found to contain any, although a species of *Ceratocystis* was on one occasion identified from fermented wood which had been allowed to dry up before examination; otherwise, the only fungi which have been found occur in the older parts of the tunnels in brown wood, where one often finds them full of a white mycelium (Pl. II, fig. 7); in such cases bracket fungi are often to be found on the outside of the trunk which have been identified as *Pleurotus hygrophanus* (Mont.) Dennis, and are evidently the fruiting bodies of the mycelium. However, the fungus is secondary, being found in rear of the advancing larvae so that there is no question of their feeding on it. The larvae live in the fermented wood, and it is here that micro-organisms closely associated with larval nutrition must be sought.

Since the nature of fermented wood suggests bacterial rather than fungal action, cultures were made from it under sterile conditions, using potato-glucose-peptone agar as a medium. In nearly all cases cultures of micro-organisms were obtained. They almost invariably form shining, whitish, semi-translucent colonies (Pl. III, fig. 1), maturing without artificial heat after two or three days. Altogether 59 samples of fermented wood were tested, mostly from different palms; cultures of micro-organisms were obtained from 52, and in the remaining cases the wood was generally much drier than usual. Smears prepared from the cultures were treated with Gram's stain and the organisms identified as far as possible.

The organism most commonly obtained was a small Gram-negative rod-shaped bacterium (type A in the list below). Some of the earlier cultures were left several days before examination, and then other types were obtained. Later, all cultures were examined after three days, or as soon as the colonies had developed, and these usually produced the Gram-negative rod-form. Of all cultures from fermented wood which produced organisms, 80 per cent. contained this form. It was by no means the only type obtained, however, for a number of others occurred either mixed with it, or in some cases without it. The various types can be included in the following seven groups, the number of cultures in which each occurred being shown in brackets.

A. Very short and small fat rods, with rounded ends; Gram-negative or sometimes weakly Gram-positive (42).
B. More elongate Gram-negative rods. Possibly the same as A (1).
C. Very large, elongate Gram-positive rods (5).
D. Medium-sized Gram-positive rods (3).
E. Gram-positive cocci (3).
F. Gram-positive yeasts; usually small and elongate but sometimes larger and round (8).
G. Fungi. Only obtained once, when spores and a few hyphae were identified.

There were nine cultures containing a mixture of two, and one a mixture of three different types. If each culture had been examined a number of times at intervals many more instances of multiple infection would doubtless have been detected. One must realise also that the culture medium selected doubtless eliminated certain types present in the original wood. The incidence of different types could not be correlated with any variable factor, such as the colour of the fermented wood. As a control, attempts were made to obtain cultures from healthy coconut wood, but this gave negative results.

One would expect these micro-organisms to enter the gut of the larva with the juice on which it feeds; cultures were only made from three larvae, one of which produced yeasts, one a mixture of yeasts with Gram-negative rods (type A), and the third rods only.

How these organisms get into the wood in the first instance is uncertain (the problem will be further discussed on p. 17). Once they are in, however, they evidently spread through the wood in advance of the larvae, as if preparing the way for them. Some graft experiments were carried out, in order to see whether fermentation could spread without the presence of the larvae. A hole of about $\frac{3}{4}$ inch diameter was drilled a foot deep into the bulb at the base of a young, healthy palm, and into it was packed tightly some humid fermented wood, without larvae, from an infested palm. The opening of the hole was plugged and the plug covered with banding grease. After three weeks the trunk was examined by cutting slices off vertically, that is to say transversely through the hole containing the graft. It was found that typical discoloration had spread in all directions (but mostly upwards and downwards) into the healthy host wood; the maximum distance of spread was $2\frac{3}{4}$ inches. This fermented wood resembled *Melittomma*-infested wood in all details (Pl. II, fig 8), including the characteristic smell. The dark border was not quite as well marked as in *Melittomma* borings. Agar cultures from the fermented host-wood produced organisms identical, in some cases at least, with those obtained from the original grafted wood.

It was found that the fermentation spread from the grafts much more rapidly in the sappy wood in the centre of the bulb than in the harder surface wood, or in the wood higher up the trunk. This is in accordance with what is found in *Melittomma* infestations, and goes some way towards explaining why infestations do not usually penetrate far up the trunk or into the hard peripheral wood (see pp. 20–21).

It would appear from this that the micro-organisms spread spontaneously through the healthy wood; one might therefore expect injections of cultures to produce similar effects, but the few experiments which have been done do not confirm this. Cultures of organisms from fermented wood were made into a suspension in 0·85 per cent. sterile saline, and this was injected with a syringe into a small hole bored into a healthy trunk with a sterilised gimlet. The opening of the hole was plugged with sterilised cotton-wool, which was covered with banding grease, and the experiments were left for a variable period before examination. The spread of infection, as shown by sectioning the gimlet-holes at various depths, appeared to be much slower than in the graft experiments; in one experiment after two months it had spread only about $\frac{1}{4}$ inch all round from the gimlet-hole into the surrounding host-wood, while in a graft-experiment after only three weeks there had been a spread of fermentation up to over $2\frac{1}{2}$ inches up and down the trunk (in all experiments the spread tends to be greater in upward and downward than in lateral directions, being no doubt carried by the vascular system). Furthermore, the nature of the infected wood round injections bore less resemblance to the typical fermented wood of *Melittomma* infestations than it did in the case of graft experiments (Pl. II, fig. 9); the colour was usually darker or sometimes a rather bright yellow, the characteristic smell was not evident and the condition was more suggestive of a normal rotting process. This was in spite of the fact that in two of the experiments a culture containing organisms of type A was used for injection, and what appeared to be the same organism was recovered from the host-wood, a yeast being also present in one of them.

There are two possible explanations of the failure to obtain similar results from grafting fermented wood and by injecting cultures of bacteria: (i) the larvae themselves may produce a secretion which influences the progress of fermentation, and which is present in the fermented wood in sufficient quantity to aid the spread of the graft; (ii) the normal fermentation may require the action or interaction of other organisms which were eliminated by the culture medium or technique adopted.

These preliminary experiments, incomplete though they are, indicate that micro-organisms (perhaps more than one species) are normally associated with *Melittomma* larvae. There is insufficient evidence to show what the precise nature of the relationship is, and how far the micro-organisms are necessary for the nutrition of the larvae. Two attempts were made to find this out: (i) by rearing eight larvae in separate blocks of wood as previously described, using in four cases fermented and in the remainder healthy wood: (ii) by feeding larvae in tubes with cotton-wool soaked in juice, extracted in some cases from fermented, and in others from healthy wood.

The first experiment was maintained for nearly six weeks, and three out of the four larvae under each treatment survived this period. The second was maintained for a fortnight, when three out of four larvae fed on unfermented juice, and three out of six fed on fermented juice, had died. These results are inconclusive, since the healthy wood or juice almost certainly acquired infection from the larvae. An interesting observation, however, was that the blocks of fermented wood did not develop any growth of moulds, even though in one case there were mycelia on the inside of the tin in which it was kept. The blocks of healthy wood, on the other hand, developed fungal mycelia, which in one case spread into the cavity in which the larva was placed. This suggests that the micro-organisms normally present in fermented wood have an antibiotic effect on fungi of some species at least, and it is possible that they maintain wood which they have invaded in a state of fermentation favourable for the larvae for a long period, thus benefiting them by postponing the normal later stages of rotting which render the wood unsuitable for them. This view is supported by the fact that in the natural state fungal mycelia which are often present in the tunnels in older, dark brown areas of an infestation never invade the fresh tunnels in which the larvae are living and feeding.

In the natural state, at all events, the larvae feed only in diseased wood which has first been invaded by the micro-organisms; this is important in considering whether the invasion of the wood by *Melittomma* larvae is primary or secondary. We shall see shortly that the larvae probably enter a trunk first and thereby introduce the organisms, and in this sense the larvae are primary. On the other hand, once the micro-organisms have gained access, they proceed through the wood ahead of the larvae, which in this sense become secondary. To put the matter in another way, the micro-organisms are the true parasites, since the larvae only feed in necrotic wood. As illustrating a somewhat similar relationship, certain termites are known which attack sound wood, but the wood surrounding their tunnels always becomes infested with fungi; in this case the same fungi are found in nature independently of termites (Hendee, 1933, 1935; Leach, 1940, p. 70 (summary)).

Larvae of a number of Cerambycid beetles are known to contain micro-organisms in and around the alimentary canal, including bacteria, yeasts and Protozoa; they are considered by some to be symbiotic, producing the enzyme cellulase which brings about the digestion of cellulose, which occurs in wood to the extent of 40–62 per cent.; they thus enable the larvae to make use of a considerable food-supply which would otherwise be unavailable; a cellulolytic bacterium has indeed been isolated in one case. The micro-organisms associated with *Melittomma* larvae may operate in a similar manner, except that instead of being confined inside the gut they may spread to the outside and into the wood, liberating simple carbohydrates which the larvae ingest in liquid solution. This might well be a natural result of the larvae feeding in humid living wood, in which the micro-organisms can survive, rather than in dry wood; the more humid it is, the further the micro-organisms can spread into it. It should be stated in connection with Cerambycid larvae, however, that other authors have found cellulase in the gut of species which do not carry symbiotic micro-organisms, so that any cellulolytic action of the latter would be superfluous. A summary of work in this field has been given by Duffy (1953, p. 10).

The benefits which *Melittomma* may confer upon the micro-organisms are more problematical, since we know nothing definite about the origin and occurrence of the latter outside the trunk. There is strong, but not indisputable evidence that the bacteria can spread without the presence of the larvae once they have gained access into the trunk, yet they do not normally attack healthy wood without the presence of the larvae, even when a trunk has been wounded by some other agency. This suggests either that the larvae assist their progress through the wood in some unknown manner, or else that in entering the trunk they introduce, among a number of others which must inevitably gain access by chance, certain specific organisms which produce the characteristic effects associated with *Melittomma* infestations. Leach (1940, p. 100) classifies the functions which may be performed by insects in transmitting and promoting the agents of plant diseases under a number of categories, of which the following may be considered here: (1) *Dissemination*, or random spreading of the pathogen from an original source; (2) *Inoculation*, or transportation to a particular part of the plant where infection may result; (3) *Ingression*, involving the entry into otherwise protected tissues, made possible through wounds created by the insect; (4) *Invasion*, enabling the spread of the pathogen through the tissues once ingress has been achieved. *Melittomma* larvae undoubtedly bring about ingression, and it is possible that in some way they assist invasion, although this is very doubtful. If the micro-organisms are specific, it is also necessary to postulate some process of inoculation; this could only be brought about through the larvae carrying the organisms at their first entry into the trunk, and the larvae in turn must acquire them through the eggs laid by the female. Instances are known in which insect eggs are infected either internally or externally with micro-organisms, and thus the larvae are automatically infected on hatching. Attempts were made on two occasions to obtain cultures from the eggs of *Melittomma*; in one case the eggs, dissected from the abdomen, were inoculated immediately on to agar with a sterilised platinum loop, and produced a culture of the typical Gram-negative short rods (type A); in the other a culture was made from the centre of a batch of recently laid eggs, and Gram-positive rods resulted (type E). This evidence, although slender, indicates that bacteria may be transmitted through the adult from one generation to the next, but far more experimental work would be required to be certain of this. No evidence has been obtained as to how the eggs may become infected, but the glutinous secretion covering the eggs, which remains moist indefinitely, offers a promising medium from which larvae may be infected at hatching. It is unfortunate that time did not allow a more thorough investigation into this and other aspects of associated micro-organisms.

Rate of tunnelling.

The rate at which larvae tunnel is of interest in connection with feeding habits. Vesey-FitzGerald estimated under natural conditions a rate of progress of eight or nine inches in eight months, which works out at rather less than a millimetre a day. Under experimental conditions in wooden blocks, however, much higher rates have been noted. When a larva is first placed in a block, the rate of progress is very rapid, but it quickly diminishes; 11 larvae after one day averaged 19·7 mm. with a range of 0–40 mm.; during the next four days they averaged 30·5 mm. or 7·6 mm. per day, with a range of 2–12 mm. per day. A single larva over a period of 70 days, during which the wood was changed several times, travelled 293 mm., averaging 4·2 mm. per day; but about one-third of this distance was covered in the first 7 days. Four ecdyses occurred during the 70 days; tunnelling usually ceases altogether during the four or five days preceding, and a day or two after, an ecdysis.

Development of Infestations in Individual Palms.

Age-groups of palms.

Early in this investigation it appeared possible that the rate of development of an infestation and therefore the severity of the attack bore some relation to the age of the tree. The exact age of a coconut palm is not always easy to determine with any precision, since the height and degree of maturity depend greatly on environmental factors as well as age. It was sufficient for the purpose, however, to distinguish certain "age-groups", and since frequent references to these will be made in the following pages, it will be well to delimit them at once. Palms of each age-group (abbreviated A.G.) can usually be recognised as follows, although borderline cases may be difficult (see illustrations on Pl. III, figs. 4–6).

A.G. I. Young palms which have not yet developed a trunk.

A.G. II. Young palms which have developed a trunk, but have not yet come into bearing. This last event normally occurs at about seven years, although it may be indefinitely delayed by poor conditions of soil and low humidity.

A.G. III. Palms between the age of coming into bearing and about 25 years. The base of the trunk is usually still soft and sappy, and has a convex bulge above the ground level. The leaf-scars are spaced well apart.

A.G. IV. Palms older than about 25 years, and up to about 60 or 70 years. The wood becomes harder and less humid with advancing age, and the base of the trunk is usually straight-sided or slightly concave as seen in profile.

A.G. V. Very old trees, older than 60 or 70 years and possibly up to 150 in some cases. Usually very tall (up to 80 feet or more), and with the leaf-scars very closely spaced.

A.G. I trees are never, and A.G. II trees seldom, attacked by *Melittomma*, and on islands where the insect exists very few palms survive as far as A.G. V. It is therefore with A.G. III and A.G. IV palms that we are almost exclusively concerned. In plantations that are badly infested, attack may start before a palm comes into bearing, but it is seldom anything but slight in palms of A.G. II; why this is so is not at all clear.

Entry of larvae.

Entry of the larvae usually occurs at or near ground level. It has been often stated that they require aerial adventitious roots for entry, and these are often present where attack occurs. This, however, is due to the habit the female has of concealing herself, before oviposition, in crevices such as roots provide; larvae can, in fact, enter the trunk at any point, and in plantations consisting largely of young trees without any adventitious roots the entry tunnels are as often as not found in smooth, healthy bark (Pl. III, fig. 2). It is true that larvae may sometimes enter through the surface of the roots, even at some little distance from the trunk, but this is the exception rather than the rule, and when attack takes place amongst adventitious roots the tunnels enter between the root-bases rather than in the roots themselves.

Larvae do not usually travel far before entering the trunk, so that a number of larvae from one batch of eggs (over 200 in one carefully investigated case) tend to enter together within a few square inches of surface. Occasionally larvae may enter some distance up the trunk, but this is nearly always in wounds such as the steps cut for the purpose of climbing the palm; this is doubtless because such wounds provide crevices to which ovipositing females are attracted. In one case in the Seychelles, infestation had occurred some twenty feet up, and in Nossi Bé (Madagascar), where the practice of cutting steps is far too prevalent, it is possible to find infestations up to nearly the top of the trunk (Pl. IV, fig. 4).

The course taken by larvae after entering the trunk is best understood when the structure of the latter is taken into account. On the outside of the trunk is a layer about ½–1 inch thick (the cortex or bark) made of tough, close-set fibres. Inside this is the wood, consisting of soft parenchyma with hard, wiry vascular bundles distributed all through it; the bundles, however, are much more numerous and close-set in a peripheral zone of about two inches thickness (Pl. IV, fig. 1); here there are usually about four or five times as many to the square inch of sectional area as there are in the centre, and this makes the wood much harder, and less humid, than in the central core (Pl. IV, fig. 2), where the parenchymatous cells contain much fluid. This outer cylinder will be referred to for convenience as the "hard ring". In older coconut trunks, and in the wild palms, the close approximation of the fibres and the hardness of the wood in the hard ring are much more pronounced than in a young coconut palm of A.G. II or III (Pl. IV, fig. 3).

When a batch of larvae enters a trunk, they usually bore horizontally at first, which takes them straight towards the centre, and through the hard ring by the shortest route. On reaching the soft central wood two tendencies are apparent. One is to turn upwards in the trunk; the other is for the individual larvae to deviate from one another, so that they tend to radiate out in all directions from a restricted source of origin. These two tendencies naturally antagonise one another to some extent; the more numerous and concentrated the larvae are at the start, the greater is the tendency to deviation, so that the lower larvae must tunnel downwards in order to deviate from the others at all; the pattern of an infestation is thus largely dependent on the number of larvae and their proximity at the point of entry. A common pattern for a heavy infestation is illustrated in fig. 9, A; one such was dissected in detail and contained 206 larvae. In smaller infestations all the larvae may turn upwards, although in one (fig. 9, B), half of the 12 larvae had turned upwards and the other half sharply downwards; this may have been due to its position some distance up the trunk, where the vascular bundles are closer together and larvae tend to get directed into the vertical columns of parenchyma between them; for although

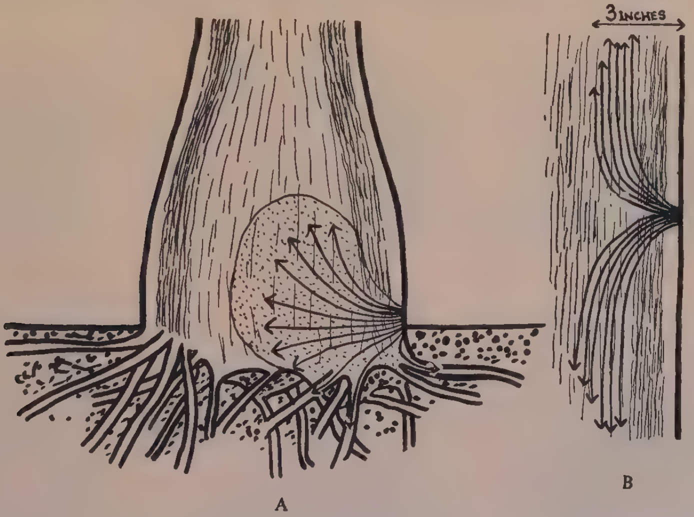


Fig. 9.—Diagrams of infestations of *M. insulare* larvae: A, typical strong infestation in a young palm; B, an unusual infestation a few feet up a trunk, with some tunnels passing upwards and some downwards. Arrows mark the course taken by individual larvae, only a few of which are shown in A.

larvae will, when necessary, bore straight through a vascular bundle (Pl. III, fig. 3), they tend to keep to the parenchyma from which they derive their liquid food. In certain wild palms, where the outer ring is very hard, the larvae seem unable to penetrate except between the root-bases, and as they work up the trunk they keep strictly to the centre, where the limited amount of parenchyma is mostly found; the hollow shell produced by long infestation is then very marked (Pl. IV, fig. 7).

Larvae may occasionally be found in roots and are then commonly thought to have entered through them, but in most of such cases their orientation, with heads away from the trunk, is the result of the direction from which they have come, for in a crowded infestation the lower larvae may deviate downwards to such an extent that their course carries them out into the root bases (fig. 9, A).

Progress of development of an infestation.

The "fermentation" and chemical breakdown which occurs in the wood round the larval tunnels has already been described. It spreads through the trunk at a rate which is dependent on the number of larvae and humidity of the wood. It has been pointed out that where both these factors are high the fermented zones round the adjacent tunnels coalesce to form a continuous mass, so that the loss to the tree of so much of its healthy, functional wood threatens to become serious. It will be appreciated from the photograph (Pl. II, fig. 5) that the greater part of the damage to the tree is caused by the microbic agents rather than the direct action of the larvae, because the former affect a far greater volume of wood.

Fermentation only spreads rapidly, however, in the interior of the trunk, and often does not permeate the hard ring, so that a peripheral cylinder of sound

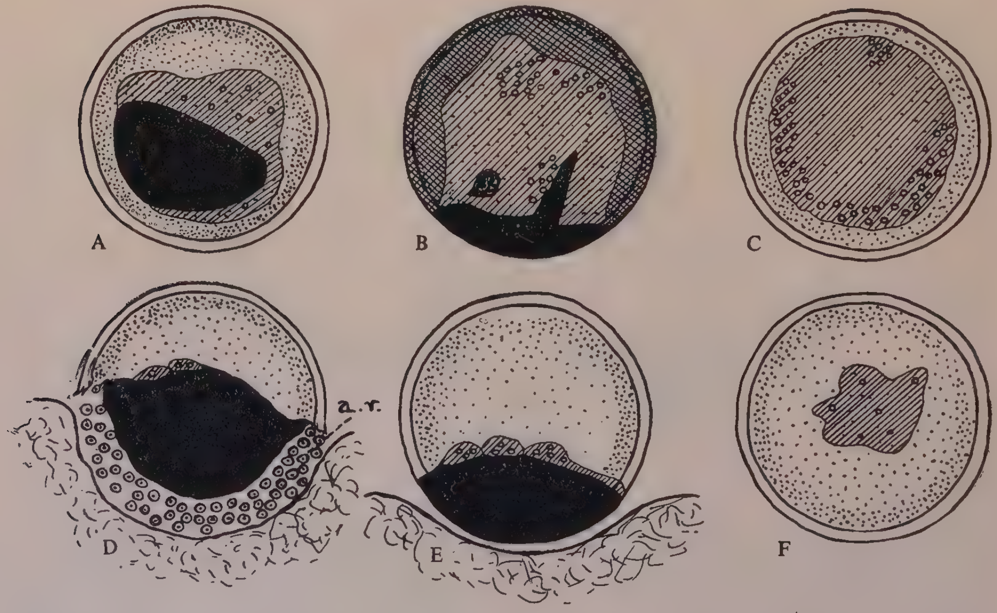


Fig. 10.—Sections of trunks, with advanced (deep) infestations showing variation in appearance at different levels. A, B, D, E are cut low down, D and E being in leaning trunks almost horizontal at the base. C and F are sections cut at a higher level in the trunk, where the infested wood has only reached the "fermented stage" (compare with fig. 11). Sound wood is indicated by dots; fermented wood by diagonal lines; reddish or brownish wood by cross hatching, and rotten wood is black. Larval tunnels are indicated by small circles. *a.r.*, adventitious roots.

vascular tissue may remain for a very long time to give the crown both mechanical support and food supplies. Furthermore, it does not often spread upwards in the interior of the trunk beyond a limit of about three feet above ground level. The reason for this is not very clear, but is probably connected with decreasing humidity, due to three factors: (a) increasing height above the basal bulb of the trunk; (b) increasing age, for unless a palm is very young when first attacked the rate of spread is so slow that it will have attained A.G. IV before the infestation has extended very far; (c) the spread of the infestation, resulting in the death of the wood at the base, which naturally restricts supplies of food and water to the wood above.

In the meantime the fermented wood (which never recovers) rots and turns black, and is attacked by a succession of other, secondary organisms, an account of which is given in a later Section (p. 42 *et seq.*). Thus the whole infestation proceeds through the trunk with an advanced zone of fermented wood followed by a zone of dark brown or black decaying wood. The diagrams (fig. 10) illustrate some typical stages in the process as seen in sectional views of trunks. The whole infestation later tends to take the form of a conical block with the zone of fermented wood over the apex and extending down the sides. As fermentation spreads further up into the trunk it slows down, and is followed up more closely by further rotting so that it is restricted to a thin apical zone.

Meanwhile the more robust of the secondary organisms, such as the larvae of *Oryctes monoceros* (Ol.), break up the rotten wood and form a hollow in the base (Pl. IV, fig. 6). When this stage is reached the number of *Melittomma* larvae is usually very small and they may die out altogether. If there is still sufficient healthy wood left the palm will continue to live and may even produce good crops, but there is always a danger that a strong gale may blow it down owing to the weakening of the mechanical support; a characteristic break occurs in the weakened walls at or just above ground level, thus exposing the central rot-filled cavity (Pl. IV, fig. 5). On the other hand, the palm may develop adventitious roots, and if these succeed in reaching and penetrating the ground they may so strengthen the weakened mechanical support as to keep the trunk standing; but many of them dry up before they ever reach the ground. These roots are probably produced as a reaction to the wound-effect of *Melittomma* attack, for they are much more numerous and extend higher up the trunks in plantations which have suffered attack over a long period (Pl. IV, fig. 8).

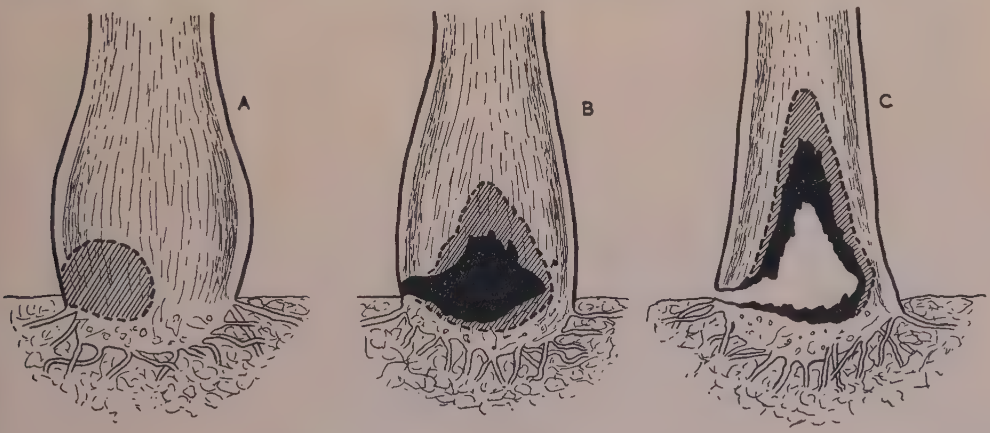


Fig. 11.—Sections of trunks showing infestations of *M. insulare* at different stages: A, superficial infestation; B, deep infestation; C, " hollow tree " stage, with central rot-cavity. " Fermented " wood is shaded, and rotten wood black. Larvae are confined to the fermented wood.

Old palms which have survived attack and are no longer infested have been referred to by Vesey-FitzGerald as " burnt-out cases." They are very common in much of Mahé, but scarcely ever survive to reach the maturity and height of the older palms found, for instance, in La Digue where *Melittomma* is absent. In areas where A.G. III palms are heavily attacked, as in Praslin, the damage is so severe that few palms reach the " burnt-out " stage.

It will be necessary, when discussing treatments for control, to be able to distinguish different conditions or stages of infestation of individual palms in simple terminology. Although one stage passes imperceptibly into another, useful broad distinctions are as follows (fig. 11).

Superficial infestation.—An early stage, where the infested wood is all still in the fermented state, without any brown or black rot; it usually involves only wood near the surface, but may extend up to about 9 inches into the trunk.

Deep infestation.—An older infestation which has extended deep into the interior of the trunk, and often upwards. It consists largely of black, rotted wood, with a zone of fermented wood round the periphery containing the larvae.

Hollow tree.—A still later infestation, which usually extends further up inside the trunk. Much of the rotten wood has been reduced to a black, powdery humus, leaving an empty cavity.

These types are characteristic of, but by no means confined to, palms of certain age-groups; superficial infestations are common in A.G. III palms, but also occur in those of A.G. IV; deep infestations often occur in A.G. III palms, but are more characteristic of A.G. IV; hollow trees are almost invariably of A.G. IV or even V. The lack of complete agreement between A.G. and stage of infestation is due to difference in intensity of attack; heavy attack in a young palm will accelerate the development of the infestation so that the later stages are attained much sooner.

The severity of the effects on the trunk depend very largely upon the total number of larvae attacking it, and also upon the number of separate batches or infestations involved. This in turn depends upon whether the eggs have been laid by one female or more, and whether each female has laid them in one batch or in several. Often one finds that all the larvae have entered in one restricted area of surface, causing rapid fermentation but less serious damage in one sense, because the greater part of the outer layer of wood is left intact. When batches of larvae have entered at a number of points, however, the effect may be very severe. In one case a palm of A.G. III had been attacked by four batches, consisting of 8, 20, 21 and 206 larvae (total 255), and distributed almost equidistantly round the trunk (fig. 12); when these infestations all spread

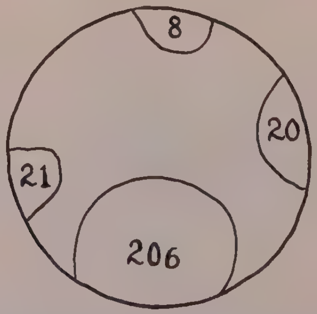


Fig. 12.—Diagram showing the distribution of four infestations of larvae of *M. insulare* in one trunk which was examined in detail; the figures show the number of larvae in each infestation.

further into the centre the destruction of sound wood must inevitably have serious results, and young palms attacked in this way occasionally die in the crown while still standing, apparently from lack of sufficient functional vascular tissue; if they do not die standing, they will inevitably soon fall owing to depletion of mechanical support. A palm may thus fall at any age; Vesey-FitzGerald (1941, pp. 391–2) made a distinction in causes between palms which fall down when old and those which fall when young; such a distinction seems unnecessary, since a palm falls from exactly the same cause at any age, namely the destruction of a considerable amount of the supporting wood, and this condition will be attained at varying ages according to the intensity of attack. This, in turn, depends largely upon the humidity of the wood. Although the year spent on this problem was insufficient to form any definite conclusions, there is no doubt that light infestations, especially in old trees, may go on for some years, the numbers of larvae never being very high; several generations may be involved, because it is not unusual to find very young larvae in the narrow zone of fermented wood above the cavity in a hollow palm; these larvae must have come from eggs laid in the cavity. An infestation of this type may be described as " chronic "; the palm suffers, but not too seriously, and survives to a fair age—perhaps 60 years.

The Progress of Infestations in a Plantation.

General outline.

Since the visible changes which occur in plantations which have become infested may occupy many years, it is impossible to give a complete account of them after only one year's observations in the islands. By piecing together evidence from different plantations, however, and more particularly from some of the smaller islands round Mahé, which appear to have become first infested at different periods, one can get some idea of the normal course of events.

After *Melittomma* has first gained access to a plantation, it may require several years before the population builds up to a high figure, due largely to the rather long life-cycle. During this incubation period, as it may be called, there may be no conspicuous evidence of the presence of the insect, other than the appearance of wood-borings expelled at the bases of the palms; but this is often missed by planters, for the apparent health of the palms and the crops are not at first impaired in any way. The small island of Conception was commonly thought to be free from *Melittomma*, but in fact on the west side almost 100 per cent. of the palms were found to be very heavily infested, and undoubtedly had been so for several years.

Sooner or later, however, palms start falling down, the strong south-east monsoon usually being responsible for the first ones. Although this has not yet occurred on Conception, it has been going on for some years on the neighbouring island of Thérèse. The damage is then plain for all to see, and the planter becomes alarmed. It may be too late by this time, however, to avoid considerable loss, for if the infestation is heavy there will be many palms, already rotten in the base, which will inevitably fall during subsequent years.

It is difficult to visualise what will happen ultimately to an infested plantation if left to itself, but doubtless some of the older palms will always survive and eventually cease to be infested, becoming " burnt-out cases." This appears to have happened on Round Island, a small, long-neglected islet off Victoria, where the few remaining coconut palms are old, and show no evidence of existing *Melittomma* but clear symptoms of former attack.

The spread from one plantation to another may be very slow, depending on chance migrations of females over distances longer than usual, and on susceptibility of the palms to attack. Instances have been noted of plantations under conditions apparently favourable for *Melittomma*, yet which are free from it or nearly so although adjacent to other plantations where the pest has evidently been prevalent for several years.

Modifying factors.

The outline of events given above is subject to modification owing to local conditions, important among which are the following:—

(1) *The age of palms in the plantation when first attacked.*—It will later be shown that young palms offer more favourable conditions for the multiplication of *Melittomma*, and in general maximum numbers are reached in a shorter time where the average age is low; this has been the case, with disastrous results, in Praslin. The insect makes slower progress in older palms. On Anonyme Island the overall percentage of palms infested is high, but there are some old A.G. V palms which show little or no sign of present or past infestation, from which it may be deduced that *Melittomma* arrived there only after these palms were old enough to resist serious attack; younger palms have suffered heavily on the island. In plantations of mixed age-group the young palms (of A.G. III) usually suffer most heavily.

(2) *Ecological factors.*—Soil or other environmental conditions which favour *Melittomma* (p. 32 *et seq.*) tend to accelerate the incubation period, and build-up of numbers is rapid. Since the same conditions are also usually favourable to the coconut palms, however, their natural recuperation is encouraged, so that in external appearance they show little evidence of the heavy infestations they carry. In conditions less favourable for the palms their recuperation is handicapped, and palms may start falling sooner, even although the numbers of *Melittomma* are no higher (Pl. V, figs. 1 & 2). In other cases, however, conditions are so unfavourable for the insect that it makes little or no headway at all; much of Amitié Estate, for instance, has virtually no *Melittomma* although surrounding plantations in Praslin have been heavily infested for some years.

(3) *Agricultural practice.*—Treatment of infested palms, accompanied by manuring and "earthing up" to encourage root-formation, and above all destruction and burning of heavily infested or fallen palms undoubtedly retards the progress of an infestation, not only by reducing the numbers of the insect but also by improving the recuperative powers of the palms. Neglect will allow a rapid build-up in numbers and, if ecological conditions favour the insect, losses will be severe. This regrettable state of affairs can be seen in many plantations in the Seychelles (Pl. V, fig. 6), and is even more striking in Nossi Bé (Madagascar), where some plantations have been abandoned as irrecoverable.

Symptoms of Attack.

Recognition of infested palms is usually easy, but not always. In view of the importance of correct diagnosis where treatment is concerned, it is necessary to deal with this question rather fully, and now that consideration has been given to the biology of the larvae and the progress of infestations it will be easier to understand the symptoms.

Recognition of infested plantations and islands.

A plantation with a high rate of infestation can often be recognised by a general appearance of dilapidation due to fallen palms; but this is not always so, because where soil conditions are good the recuperative powers of the palms may be so high that little damage can be seen, even although a high percentage of palms have been attacked (Pl. V, figs. 1 & 2).

Palms can, of course, fall from causes other than *Melittomma* attack, but an examination of the base of the fallen trunk will put the matter beyond doubt.

A palm attacked by the insect typically breaks across the weakened wall round the rot-cavity, at ground-level or up to about a foot above it (Pl. IV, fig. 5). The black, rotten wood in the cavity is exposed, and the majority of the roots are left in the soil. All fallen palms in non-infested islands, which have usually been blown down by the wind, are either completely uprooted or else snapped off some distance up the trunk (usually about half way). This distinction is useful in determining whether an island as a whole is infested or free from the insect.

Plantations of old palms which have suffered attack for many years are characterised by heavy growth of adventitious roots (Pl. IV, fig. 8), often extending some three or four feet up the trunk.

Recognition of infested individual palms.

In examining individual palms there is no single symptom which can always be relied upon, and one has to examine several possibilities.

Examination of the base of the trunk.—There are certain *external* signs which should be looked for first.

(a) Borings.—At or below the entrance to the tunnels the borings of the larvae may be found, yellowish when fresh but turning brown after some time; typically they have the appearance of sawdust, compacted into small, spherical or oblong pellets of up to about 3 mm. diameter, depending on the size of the larvae. There are other insects which produce borings, but these are usually either in the form of long thin strings hanging from the tunnels (*Xyleborus*) or of fine dust; the pellets of *Melittomma* may also get broken down to dust, and it is always best to confirm suspicions by searching among the borings for the hoof-shaped cast tail-pieces of the larvae (Pl. I, fig. 3), which are very persistent. Heavy rain may wash borings away so that in small infestations there is nothing to see. Furthermore, it is only in " superficial " infestations that larvae descend right to the surface of the trunk to cast out their borings. Absence of borings therefore cannot be regarded as decisive evidence of absence of larvae.

(b) A rusty coloration of the bark at the base of the trunk, or an exudation of gum, or both, sometimes signify the presence of larvae, but may result from other causes. They arise through the escape of fluids from the tunnels, the rusty coloration being produced by oxidation of sap.

(c) Hollows in the trunks with older infestations can sometimes be detected from the outside, either through external openings, or through black, rotting wood-débris pushed out by the larvae of *Oryctes* or other animals. They are, however, not always visible, especially in the earlier stages of " deep " infestations and since the larvae do not descend through wood in advanced stages of rotting their borings may never reach the outside, and there is nothing to see.

(d) When a trunk containing larvae is struck sharply with a hard object the larvae often start making a grating noise which can be heard by holding the ear close to the trunk. It is probably made by the larvae biting on the hard vascular bundles; since they are often surrounded by soft parenchyma tissue without access to a bundle, not all larvae will be in a position to perform at any one time, and as a method of detection it cannot be relied upon.

In fact none of the foregoing symptoms can always be relied upon. Any one of them may give positive evidence, but even if they all give negative results this should not be regarded as final. In cases of doubt it is best to make an *internal* examination by shaving away a little surface wood at suspicious points round the base of the trunk with a small axe or heavy knife, and look for the following symptoms:—

(e) The characteristic appearance of the tunnels surrounded by zones of fermented wood (Pl. II, fig. 5) will be evident in superficial infestations and the larvae themselves will usually be exposed.

(f) In older infestations the removal of surface wood will expose the central hollow, which may or may not be filled with dark brown or black wood in various stages of decomposition.

Examination of the crown and the top of the trunk.—Damage at the base of the trunk may under certain circumstances be reflected in reactions at the apex and in the crown, and there are two types of symptoms here which have been attributed to *Melittomma* attack.

(a) Tapered trunk.—In poor, dry laterite soils such as one frequently finds on exposed hillsides, coconut palms grow slowly, finding increasing difficulty in obtaining sufficient nourishment; the trunk consequently becomes constricted at the apex to varying extents and the crops become seriously impoverished; in extreme cases the palms may die (Pl. V, fig. 4). This tapering has in the past been attributed to *Melittomma* attack. The incidence of the insect in such palms will be discussed later (p. 35), but there is no doubt that Vesey-FitzGerald over-estimated its importance as a cause. On one hillside at Anse Boileau, where the tapering and stunting of trunks was more marked than anywhere else, palms 25 years old were found with conical trunks only one foot high (Pl. V, fig. 3); when the whole plantation was cut down with a view to terracing the soil, not a single palm was infested, the wood being sound throughout. In Kenya, where coconuts are not attacked by *Melittomma*, an exactly similar tapering effect can be seen on dry soils to the west of Mombasa. In such soils, therefore, one cannot regard constriction of the trunk as evidence of *Melittomma*, but this does not mean that it does not in some cases act as a contributory factor. In fertile soils one very rarely finds a constricted trunk, but there are grounds for supposing that, in the instances when one does, *Melittomma* may be an important cause; one sometimes finds a single tapered trunk among a lot of well-grown palms, and examination of at least one such case has showed it to be heavily attacked. One often finds palms with constrictions half way up the trunk, which are attributed to past attack and subsequent recuperation, but it is difficult to establish the authenticity of these statements.

(b) Dying-off of the crown.—The foliage and terminal bud can die from varying causes, either direct attack by organisms on the crown itself, or indirect action consequent upon the deterioration, for one reason or another, of the roots or trunk base. It is therefore very difficult to diagnose the cause of a dying crown, although the precise symptoms may vary. For instance, the leaves may die from the base of the crown upwards (the oldest first), or from the top downwards. The former is a rather uncommon but very characteristic condition in the Seychelles (Pl. V, fig. 5); the lower leaves first collapse round the trunk, breaking across the petiole typically about 1–2 feet out from the base, without becoming severed. Then the leaves immediately above them follow suit, and so on until there remains only a tuft of the youngest leaves standing erect in the centre. The nuts are often very attenuated and reduced in size. Ultimately the whole crown dies and falls off. This condition was described by Vesey-FitzGerald (1941, p. 392), who regarded it as the result of an acute attack by large numbers of larvae in a young, sappy palm. This does indeed appear in some cases to be true, and one supposes that a heavy attack may ferment and kill so great a volume of wood that the crown is physiologically cut off from the roots; it is difficult to see how else an attack could cause the dying off of the crown. But yet if this is so one would expect the effects to show first in the tender terminal bud and not the older leaves. A number of these palms were examined in detail, and in many there were very few larvae and often none at all, although one of these was heavily attacked by the Scolytid beetle *Xyleborus confusus* Eichh. Furthermore, in the island of La Digue, which is completely free from *Melittomma*, some very typical instances of this condition were found.

It is thus evident that *Melittomma* is by no means the only cause of dying-off in the crown; it is very probable that the symptoms described above have another principal cause altogether, although naturally the effects may be accentuated, as in the case of tapered trunks, by concurrent attack by the larvae.

Occurrence in Native Palms.

The interest attached to the breeding of *Melittomma* in native palms was discussed by Vesey-FitzGerald, who demonstrated its occurrence in two of the six indigenous species (*Stevensonia* and *Nephrosperma*). Some attention was given to this question in the present investigation, not only for the theoretical interest, but also in order to ascertain how important the palms in question might be as a reservoir, from which the beetle would always be capable of re-infesting coconut plantations. An account follows of the observations made for each species of palm (four in all) in which breeding has been found.

Stevensonia borsigiana (K. Koch) L. H. Bailey. ("Latanier feuille").

This is unquestionably the most important species, both on account of its abundance and distribution and the extent to which it is attacked by *Melittomma*; it is abundant on all the main granitic islands, and over a wide range of altitude, including the lower levels, where the main distribution of coconuts and of *Melittomma* lies. The trunk is seldom more than 10 feet high, and the roots arise from its swollen base at or a little below ground-level. *Melittomma* larvae appear only able to enter the trunk between the root-bases, the outer layers of the trunk higher up being too hard. Although quite old palms, with trunks up to seven or eight feet high, may contain larvae, it is probable that initial attack only occurs in young ones with a trunk about one foot high. The trunks of older infested palms are hollowed out or rotten in the centre nearly up to the top (Pl. IV, fig. 7), with only a thin outer shell of sound wood remaining, and they are often stunted or tapered—all these symptoms indicating prolonged attack over a number of years.

A number of sample counts were made in palmeta in different places to estimate the percentage of palms attacked, with the following results:—

Mahé:

(i) Cape Ternay, 2.iii.1952, 9 per cent. (30 examined).
(ii) Montagne Posée, Grande Anse, 28.iv.1952, nearly 50 per cent. (16 out of 33 examined).
(iii) Sancta Maria, Canelles, 20.v.1952, 24 per cent. (25 examined).

Silhouette:

(iv) Anse Patate, 12.iv.1952, 0 per cent. (10 examined).

In addition, casual examinations, without taking counts, were made on numerous occasions, and infested palms were found in other places on the Canelles Road, at Cascade (Mahé) and on Thérèse Island. The number of larvae in a palm is never high, four being the maximum recorded. In one palm, however, some 30 separate tunnels were dissected out, but many of them seemed to be abortive, being devoid of larvae although still very short. Usually one finds one or two living larvae in the base of a very young trunk, or in the limited zone of fermented wood above the rotting centre of an older one; often, however, no living larvae can be found although their tunnels remain as a testimony to earlier attack.

Nephrosperma vanhoutteana Balf. f. ("Latanier hauban").

This palm often has short adventitious "stilt-roots" coming off near the base of the trunk. It is especially common on Silhouette, where the only instance of infestation was noted; about seven tunnels, each 7–9 inches long; and with larvae in two of them, were found in the stilt-roots of one of a stand of half-a-dozen palms. No other instance was found, but few palms of this species were examined.

Deckenia nobilis Wendl. (" Palmiste ").

Samples were examined in stands on Silhouette (20 palms) and Praslin (25 palms), and numerous scattered palms were investigated in various places. In only one instance was infestation found, in a palm on Thérèse Island with a trunk 7–8 feet high. The trunk had a large hollow extending about half way up from the base, filled with much rotten black wood. Only two or three living larvae were found, in the roof of the hollow. The attack must have been working up the trunk for a considerable time. The wood of full-grown palms of this species is very hard and unfavourable for *Melittomma* larvae.

Roscheria melanochetes Wendl. (" Latanier mille-pattes ").

This is a small mountain-palm, not commonly found except on the mountain-tops of Mahé and Silhouette at or near 2,000 feet, and usually above the highest coconuts although sometimes not separated from them by any great distance. Only once was a trunk found to be infested, at 2,000 feet on Morne Pot-à-eau, Silhouette. The trunk was only four inches in diameter at the base and about 3 ft. 6 ins. high, with a tapered top, and a rot-filled hollow extending two-thirds of the way up. When cut across at about 15 inches from the base, 16 tunnels could be seen in section, but a careful dissection of one half of the trunk only revealed a single larva, a second one later crawling out of the other half. Another palm near the first was tapered and stunted almost as much, and had a central rot-cavity, but there were no tunnels; probably an earlier attack had died out.

The only other native palms in the Seychelles are *Lodoicea maldivica* (Gmel.) Pers. (" Coco de mer ", " Double coconut ") and *Verschaffeltia splendida* Wendl. (" Latanier latte "), in neither of which has *Melittomma* been found. The wood of the former is much too hard and dry to offer favourable conditions, while the latter usually has very long stilt-roots which would make entry into the base of the main trunk difficult.

In addition to wild palms there is also a report of larvae from cultivated areca-nut palms (*Areca catechu* L.).

In Madagascar a number of palms of *Hyphaene schatan* Boj. and *Raphia ruffia* Mart. were examined, with negative results; the wood of the former is exceedingly hard and dry.

Summarising this evidence, one may say that most wild palms do not offer favourable conditions for larvae of *Melittomma*, but that occasionally it may gain a precarious footing in those species in which the wood is less hard and dry. The mortality, however, is very high to judge from abortive tunnels and the small number of living larvae found.

Geographical Distribution, Origin and History.

Melittomma insulare is known only from some of the granitic islands in the Seychelles (fig. 13) and from Madagascar.

In the Seychelles we have found it during the present investigation in the following islands:—Mahé and all its satellite coconut islands examined (St. Anne, Moyenne, Long, Cerf, Île Cachée,* Anonyme, South-East, Thérèse and Conception); Praslin; Silhouette. The only satellite island of Mahé where it was not found was Round Island, but here only a few very old palms remain, and there is evidence of past infestation. Other granitic islands we have examined, but with negative result, are North Island, Récif (where only two or three coconut palms now remain), and many of the satellite islands round Praslin (La Digue, Félicité, Grande Soeur, Aride, Cousin and Round Island). The Praslin satellites we have not examined are Petite Soeur, Marie Anne and Cousine, which are said to be free from the pest. Frigate Island is also said to be free, but there is no reliable recent report on it.

---

* A very small islet off the south-east end of Cerf.

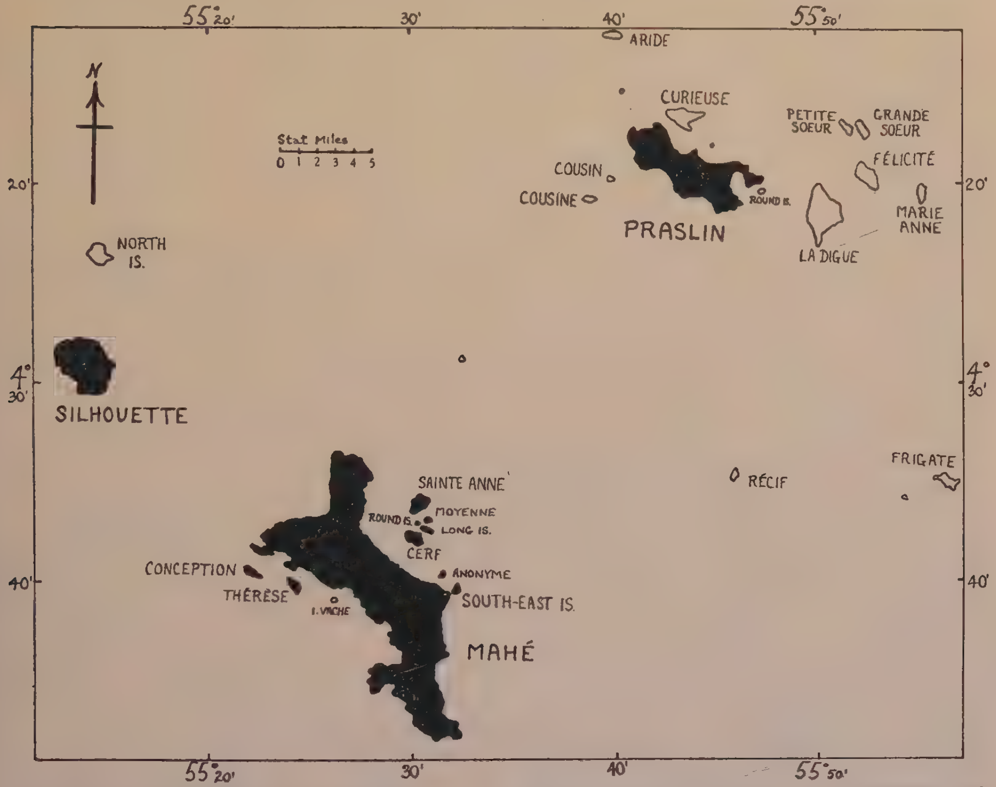

55°20'
30'
40'
55°50'
ARIDE
N
CURIEUSE
PETITE SOEUR
GRANDE SOEUR
Stat Miles
0 1 2 3 4 5
FÉLICITÉ
20'
COUSIN
COUSINE
ROUND IS.
PRASLIN
MARIE ANNE
LA DIGUE
NORTH IS.
4° 30'
SILHOUETTE
FRIGATE
SAINTE ANNE
RÉCIF
MOYENNE
ROUND IS.
LONG IS.
CERF
CONCEPTION
ANONYME
40'
THÉRÈSE
I. VACHE
SOUTH-EAST IS.
MAHÉ

Fig. 13.—Map of the granitic islands of the Seychelles group, showing the distribution of *M. insulare*. Islands in which it occurs, or in which there is evidence of past occurrence, are blacked in.

There is an old record from one of the coral islands, namely Desroches in the Amirantes group (Scott, 1926), but there is no recent confirmation, nor is it likely to have escaped recent detection if it really exists there. Ecological conditions on the coral islands are most unfavourable for it, and there was no sign of it on several others that we have examined, namely Île Platte, Marie Louise, Farquhar, Astove, Glorieuse.

In Madagascar, it is known certainly only from the north-west. The writer found it in the islands of Nossi Bé and Nossi Comba, and in the following districts on the mainland:—the coastal flats of the Sambirano area around Ambanja, including also small scattered village plantations extending up into the hills as far as Bemanevika; the peninsula of Ambato farther north; and in small numbers in plantations to the south of Ambilobe. To the north of Ambilobe, and right through the high ground of the Anivorano district as far as Diego Suarez at the northern extremity of the island, it was not found, and suggestions will later be given to account for its absence (pp. 37, 38). Frappa (1948) states that it extends farther south as far as Analalava and the island Nossi Berafia, and north to " la hauteur d'Anivorano ", which would limit its distribution between Latitudes

14°15′S. and 14°38′S. But it is doubtful if it exists as far north as Anivorano, unless it is in the coastal districts. There are also unconfirmed reports from the Comoro Islands on the west, and from the island of St. Mary on the east side of Madagascar.

The distribution in the Seychelles is very curious and difficult of explanation, in that all the satellite islands round Mahé are either infested or show signs of former infestation, while those round Praslin are quite free. Even Round Island, which is only about 400 yards from the Praslin mainland, is free from it, although conditions appear to be suitable. A small sea barrier usually seems to be very effective, for Curieuse also is no more than a mile distant from Praslin. This is doubtless due to the poor abilities of the female in flight, but it has been pointed out earlier that females do occasionally fly more strongly than usual, and it is not impossible that the coincidence of a suitable wind might on extremely rare occasions blow one from one island to another.

Moreover, there is evidence that some of the satellite islands of Mahé have not always been infested. It is said that Thérèse was free from *Melittomma* in the year 1909, but now it is very heavily attacked. Conception also is heavily attacked now, but apparently since a later date, for while many palms are now falling on Thérèse as a result of prolonged infestation, there are few if any fallen palms on Conception. Anonyme is unique among infested islands in that there are a number of very tall palms of age-group V, reminiscent of some of those on La Digue; none of these are hollowed out as one would expect if they had been long attacked; one would judge them to have been free from attack when young and susceptible; the younger palms, on the other hand, are very heavily attacked. It is therefore probable that the pest gained access to Anonyme only since the older palms had got past the susceptible younger stages. An old inhabitant of Cerf Island states that there was no *Melittomma* there until it appeared some 45 years ago; this story is supported by the fact that now there is heavy infestation on the north side where it is said to have been first introduced, but very little on the south.

It is thus not improbable that the beetle was introduced into Mahé at some time in the past, prior to 1900, and has since been spreading to the satellite islands at varying intervals of time, and possibly also to Praslin and Silhouette, either by human agency or through the rare coincidence of a more active female crossing the sea by flight. But why the satellites of Praslin have thus far remained immune is a problem which cannot be solved on present evidence.

We must now turn to the question of the history of *Melittomma insulare*, and the light thrown on it by present distribution and other evidence. Specimens from the two distinct parts of its range, Madagascar and the Seychelles, have been carefully compared, by external examination and by dissection of genitalia, and no difference can be found between them. It is unlikely that two such isolated populations would remain conspecific for the long period which must have elapsed since the separation of these two land masses, and it seems probable that the species evolved in one and recently gained access to the other, most likely by human agency, since it is difficult to see by what other means it could have occurred. If this view is accepted, it is of interest to speculate whether it reached the Seychelles from Madagascar, or vice versa. It was first discovered in the Seychelles in 1893, and in Madagascar in 1911; but this in itself means little, because owing to its habits and life-history it might easily remain long undetected unless common enough to do conspicuous damage. In fact, Dupont (1938) states that its existence had been suspected in the Seychelles for about half a century before the Government recognised it as a pest in 1903.

The evidence must therefore come from two main sources—breeding in native palms, and present distribution. Vesey-FitzGerald has maintained that it is indigenous in the Seychelles, where it was originally a parasite of the endemic palms and only later transferred its attentions to coconuts. This view is reasonable, but is difficult to accept when one realises that the whole mode of nutrition of the larva seems to have evolved as an adaptation to life in sappy wood such as that of a coconut rather than the drier wood of the native palms. It seems much more likely that it evolved as a coconut parasite and that it sometimes accidentally gets into the less favourable environment provided by other palms, where it only ekes out a very precarious existence. On the other hand one can maintain that the severe effect of the parasite on the coconut palm indicates a comparatively recent relationship between them. Vesey-FitzGerald pointed out that the distribution of the insect in the Seychelles offers some support for the theory of a wild palm ancestry, because it conforms in some ways with that of the endemic palm forests. The discovery of larvae in *Roscheria* (p. 28) on the mountains high above the coconut line is significant in this connection, although palms of other species occurred in the intermediate zone. There are, however, some facts which do not fit very well. For instance, there is no *Melittomma* on Curieuse, although one of its indigenous palms, *Deckenia nobilis*, is an occasional host. Moreover, if the beetle originated in the native palm forest on Mahé, Silhouette and Praslin, how is it that it now exists on all the satellite islands of Mahé but on none of those of Praslin, although some of the former have no more evidence of ancient palm forests than have, for instance, La Digue and Félicité?

This curious distribution is difficult to explain on any grounds. At first it seems to support the view that *Melittomma* was first introduced into the mainland of Mahé, since when it has found its way to Praslin and Silhouette and to all the satellites of Mahé.

The question depends obviously to some extent on whether the coconut is indigenous in the Seychelles. Bradley (1940), although he enumerates it in a list of introduced species (and Vesey-FitzGerald apparently accepts this view), states elsewhere in his work that when the "Elizabeth" and "Le Charlie" reached the Seychelles in 1742 on a voyage of discovery they found no inhabitants, but "the sea-shore was lined with coconut trees". If in fact coconuts already existed in the islands there is less to support the wild palm origin.

In support of the view that the beetle originated in Madagascar and later reached the Seychelles, is the fact that other species of *Melittomma* occur in Madagascar, which is thus more likely to have been a centre of evolution in the genus. From the known distribution of *M. insulare* in Madagascar there is no evidence to suggest that it has not had plenty of time to colonise all areas which are suitable for it. It is found not only on islands off the coast, but was encountered on the mainland in a number of small and quite isolated village plantations. It was already serious as a pest by 1912, and many years would have been necessary for it to have reached such importance and wide distribution.

Always assuming that the beetle originated in one country and later reached the other, it is not easy to understand how the journey was made; but it would have to be in the larval stage, since the other stages are not of long enough duration for the transport which existed then, and would almost certainly have been in trunks or logs of coconut or another suitable palm. There is no evidence that coconut wood was ever shipped between Madagascar and the Seychelles, and even larvae would be unlikely to survive in a floating log.

It is clear from what has been said that such evidence as there is regarding the past history of this pest is highly conflicting and does not enable one to arrive at any definite conclusions.

Ecological Factors in Distribution.

Throughout the present investigation an attempt was made to correlate the incidence of heavy populations of *Melittomma* with local environmental factors.

With this object, apart from casual observations on local conditions, a large series of sample counts were made to estimate the percentage of palms infested in different plantations. These plantations were selected to give fair representation to all the varying conditions of soil, geological and topographical formation under which coconuts are grown. In the majority of cases, since approximate estimates were judged to be sufficient, a random sample of 33 palms was examined, taking care that all the palms fell within an area where conditions were apparently homogeneous. The number of infested palms was then multiplied by three to give an approximate percentage. In a few cases it was necessary to work with smaller samples, while in others larger samples of 50 were used.

The initial problem was to decide what were the important ecological details to record among the local conditions. Of edaphic factors, soil type was obviously likely to prove important, as had been found earlier to be the case by Vesey-FitzGerald (1941); it soon became apparent that steepness of slope and topography in general were likely to be of importance also in that they influenced conditions of soil humidity; it was unfortunately impracticable to measure the latter precisely, because it varies greatly at different depths, and according to seasonal and prevailing weather conditions. Biotic factors did not seem important at the outset, but records were kept of associated plants, and of certain associated animals which might have some ecological relationship with *Melittomma.* It soon appeared that the age of the palm was likely to prove important, and so the age-group of every palm in a sample was recorded. Fallen palms were included in samples where the fall was due to *Melittomma* and a record was made of hollow palms to give an idea of the periods for which plantations had been infested. Altogether about 120 samples were recorded in the Seychelles, and 36 in Madagascar.

A discussion of the results of sampling follows, but only those factors which proved to be most important are included in this analysis.

Soil-types.

Vesey-FitzGerald (1940, pp. 255–259) has enumerated the types of soil in which coconuts are grown in the Seychelles. His three main categories have been retained, although the minor classification has been modified slightly for present purposes. In the discussion which follows, the reference letters and numbers used are those given in Table IV.

A. *Coral sand or " rendzina " soil.*—This occurs on the narrow coastal plains or "plateaux" round the shores of the granitic islands, and is the best for coconut plantation. An account of the qualities of this soil has been given by Lionnet (1952). The soil is very porous and drains readily.

B. *Alluvial soils.*—It has been considered unnecessary to distinguish between all the variants of the alluvial soils given by Vesey-FitzGerald, since what appears to be important in the present study is not so much the alluvial soil itself but the conditions which promote its formation, and these are much the same. The alluvial soils round the marshes at sea-level, however, have been distinguished from the hillside alluvia because it is of importance to compare infestation in the former with that in closely adjacent rendzina soils at the same level.

(i) Marsh areas at sea-level.—Under the foothills at the back of most of the coastal plains is a marshy area, where the soil is much wetter and poorly drained, and silt washed down from the heights has formed a superficial layer over the coral sand. Marsh conditions have usually resulted in the accumulation of an appreciable amount of humus, and a lush ground vegetation is frequent.

(ii) Hill-side valleys and talus-slopes.—In the troughs of the larger valleys and ravines running down from the heights to the coastal plain there is usually a certain amount of silt, especially in flatter stretches where the erosive action of running water is not so severe. Near the bottom of a valley alluvial soil may build up to form a talus-slope, often adjacent to but raised above the level of the plateau marshes.

C. *Sedentary lateritic soils on hillsides.*—The hillside soils, which support by far the greatest acreage of coconuts, have a basis of laterite or "red earth"; but there is a great range of variation in their exact nature, depending on the extent of erosion on the one hand, or of stability and consequent humus-formation on the other; also, owing to the precipitous nature of many of the slopes, there may be small admixtures of alluvial matter washed down from the heights, although insufficient to classify them as alluvial soils. These features are difficult to measure, and it has been considered wisest to make a purely arbitrary distinction into two categories:

(i) "Tuffes," in which erosion is considerable, and exposures of red laterite are conspicuous, the vegetation cover being locally depleted. These are the worst soils for coconuts in the islands; they are very characteristic of Praslin and Curieuse, where hillside coconut culture is very reduced as a consequence.

(ii) Soils with more humus.—These are characteristic of the smaller valleys and re-entrants, or of slopes with many very large boulders (Pl. VI, fig. 6) which arrest erosion and between which pockets of brown loam accumulate. Their qualities as coconut growing soils vary directly with the extent of this humification. Small but variable amounts of silt are usually mixed with the soil to form the characteristic gritty loams, so that it is sometimes difficult to differentiate between them and the hillside alluvial soils; failure to draw sharp distinctions in a few individual instances was not serious, however, since incidence of *Melittomma* in soil-types B (ii) and C (ii) did not differ very markedly.

An analysis of the infestation rate, as judged by the percentage of palms infested in samples, raises various points of interest (see Tables III and IV).

TABLE III.

Average values and extreme range of variation in percentages of infestation, in plantations on different soil-types.

	A Coral sand	B Alluvial soils		C Sedentary soils on hillsides	
		(i) Marsh-areas at sea-level	(ii) Hillside valleys and talus-slopes	(i) "Tuffes"	(ii) Soils with more humus
Number of samples	24	14	21	15	45
Extreme range in percentage of palms infested	0–88	0–87	18–100	0–93	0–97
Average percentage of palms infested	19·50	50·00	52·76	25·93	40·91

The first point which strikes one is that almost the maximum overall range of variation occurs within every individual soil-type (Table III); this alone seems to indicate that soil-type by itself is a factor by no means limiting distribution of *Melittomma*; but yet in average values there are some marked differences which require attention.

Plantations on coral sand plateaux (A, p. 32) are on the whole more free from attack than those on any other. Of the 24 samples recorded, 6 showed 0 per cent. and 15 showed 12 per cent. or under. This is especially true of Mahé,

TABLE IV.

Comparison of percentages of infestation in plantations on different soil-types, and in different islands.

Islands	A. Coral sand			B. Alluvial soils						C. Sedentary lateritic soils on hillsides						Totals (All soil types)		
				(i) Marsh-areas at sea-level			(ii) Hillside valleys and talus-slopes			(i) " Tuffes," dry hills with exposures of red earth			(ii) Soils with more humus					
	No. of samples	Total added percentages infested	Average percentage infestation	No. of samples	Total added percentages infested	Average percentage infestation	No. of samples	Total added percentages infested	Average percentage infestation	No. of samples	Total added percentages infested	Average percentage infestation	No. of samples	Total added percentages infested	Average percentage infestation	No. of samples	Total added percentages infested	Average percentage infestation
Mahé	10	90	9·00	7	222	31·71	14	660	47·14	12	225	18·75	31	1214	39·03	74	2411	32·58
Praslin	7	226	32·29	6	478	79·67	3	156	52·00	1	93	93·00	2	128	64·00	19	1081	56·89
Silhouette	1	0	0·00	—	—	—	1	33	33·00	2	71	35·50	2	47	23·50	6	151	25·17
Small islands round Mahé	6	152	25·33	—	—	—	3	259	86·33	—	—	—	10	452	45·20	19	863	45·42
All islands together	24	468	19·50	13	700	53·84	21	1108	52·76	15	389	25·93	45	1841	40·91	118	4506	38·18

where the maximum found was 36 per cent. The overall average was considerably inflated by a few abnormally high values from Praslin, where general infestation is so high that large numbers may occur under almost any conditions; even on Praslin, however, the only two plantations free from *Melittomma* were on coral sand.

Alluvial soils (B, p. 32) undoubtedly provide the conditions most conducive to attack, no matter where they may be found, on the coastal plains or in the hillside valleys. Average values are 50 per cent. or more. The marshes at sea-level are very characteristic of Praslin, where the average of 79·67 is largely responsible for the high overall value for this island.

Plantations on the sedentary soils on hillsides (C, p. 33) show the greatest variability in extent of attack, and almost half the total number of samples were made from this source. There is a marked difference between the barren, eroded "tuffes" and the soils with more humus content, the former being much less heavily attacked. The average for type C (i) soils for Mahé is only 18·75, 6 of the 12 samples showing less than 15 per cent., and the highest 56 per cent.; but here again the overall average is inflated by a large value of 93 per cent. from one Praslin sample, where, although erosion is much worse than in Mahé, there are very few plantations on tuffes because planting is unremunerative. On more stable soils, where the humus content is higher, attack is much more serious. Taking the figures for Mahé alone, where most of the hillside sampling was done, we find that the average values for soil-types C (ii) and C (i) are 39·03 per cent. and 18·75 per cent. respectively, a difference of over 2 : 1. Moreover, the number of larvae per tree on the tuffe soils is generally much smaller.

Humidity and factors affecting it.

It soon became evident that humidity was a point of major ecological significance, and in view of the method of feeding of the larvae and its relation to fermentation of the wood described earlier, it would appear that any factors promoting high humidity in the wood during all or part of the year should be of paramount importance. Attention was therefore given to such factors, among the most important of which are the following :—

Topography of the land.
Type of soil.
Rainfall.
Drainage.
Age of palm.
Associated vegetation.

These will now be discussed in turn.

Topography and type of soil.

These may be conveniently discussed together. The formation of land is important in that it directs and regulates the movement of water through the soil, concentrating flow and soil humidity in some places and impoverishing it in others. This in turn largely determines the types of soil which develop in different localities, and one finds that the soils in which infestation is highest are those which develop under conditions of highest humidity. Thus, the alluvial soils associated with heaviest attacks develop as the direct result of the distribution of water courses, and in a general way may be regarded as having water passing through them in greater quantity and for a longer period of time.

In order to obtain evidence of the importance of humidity, a practice was made of taking separate samples on two adjacent areas which obviously differed in water content of the soil but in little else. The results of all such observations, including two from Madagascar, are summarised in Table V, where the two samples of each pair are placed opposite one another. Many of them are certainly

TABLE V.

Comparison of percentages of palms infested in closely adjacent areas, soil conditions in one area of each pair being drier, the other more humid.

Ref. number	Locality	Drier conditions		More humid conditions	
		Nature of locality	% palms infested	Nature of locality	% palms infested
1	Anse aux Pins, Mahé	dry coral sand, at some distance from marsh	3	narrow strip beside ditches in marsh; soil more alluvial	21
2	La Province, Mahé	as above	0	coral sand alongside marsh, with admixture of loam	42
3	Vale Mer, Mahé	as above	0	coral sand; single row of palms alongside marsh, but raised somewhat above it	12
4	Amitié, Praslin	coral sand, in dry part of the coastal plain	0	coral sand nearer marsh, with more humus on surface	9
5	Anse aux Pins, Mahé	coral sand, with much black loam; distant from marsh	6	coral sand with much black loam; row of palms alongside marsh	36
6	Ambato, N.W. Madagascar	dry area of white sand	4	soil more moist, close to ditches	16
7	as above	flat, white sand, second row of palms back from swamp	23	single row of palms alongside mangrove swamp	76
8	hills above Anse-la-Mouche, Mahé	dry laterite, soil largely exposed	12	gritty loam, at head of ravine	78
9	Cascade, Mahé	hillside; gritty loam between boulders	27	hillside valley; gritty loam alongside stream	75
10	Béolière, Mahé	loam, fairly moist, slightly raised	9	loam; in trough of watershed	39
11	Anse Major, Mahé	hillside; gritty loam between boulders	36	ravine; very damp soil with much detritus	59
12	Anse Boileau, Mahé	dry coastal plain; soil largely alluvial loam with sand locally	0	wet, marshy coastal plain; mostly alluvial; muddy loam locally	45
13	Baie St. Anne, Praslin	talus slope, alluvial, fairly dry	54	coastal plain, alluvial, wet, beside marsh	63
14	Pasquière, Praslin	alluvial; a raised mound, soil dry	39	coral sand; low-lying, alongside marsh	88

very striking. In several cases (nos. 1–7) samples were taken from the drier part of a coral sand plateau on one hand, and from a more or less narrow strip of the same plantation alongside a marsh on the other; in all cases the proximity of the marsh raises the percentage of palms attacked; in many cases there is a difference in soil-type, alluvial soil appearing alongside the marsh, but in others this is not so, both areas being of coral sand and the proximity of the marsh being the only apparent difference. One of the instances from Madagascar (no. 7) involves a plantation alongside a large mangrove swamp; a single row of palms next to the swamp was over three times as heavily infested as the next row back from it; the samples in no. 6 are from the same plantation, but in the centre of it and far removed from the swamp, and they show still less attack. In other pairs of samples (nos. 8–11) plantations on dry lateritic soil on convex hill slopes are contrasted with those in the adjacent troughs or re-entrants at the same altitudes; the latter show infestation-rates averaging three times those of the former. In examples 12 and 13 alluvial soils are involved in all cases, but there were obvious differences in humidity depending upon one area of each pair being raised a few feet higher.

Perhaps the most significant case of all was at Pasquière in Praslin (no. 14), involving two soil-types, coral sand and alluvial; the infestation-rate was exactly the reverse of what one would expect to find, being over twice as great on the coral sand as on the alluvial soil. The reason appeared to be that the alluvial soil, which had evidently been formed as a talus slope, had in some way become isolated as a mound, raised slightly above the low plateau all round it; so that unlike normal talus-slopes the water would drain out of it without being constantly replaced from the slopes above. The adjacent coral sand area in this case was low-lying, alongside a marsh so that the water-table was relatively high. This instance strongly supports the view that although there is a relation between soil-type and *Melittomma* distribution, the important factor is humidity, which in unusual circumstances will override any direct soil factors there may be. Putting the matter in another way, soil-type is probably not a direct factor determining *Melittomma* distribution, but rather the distribution of the insect and of soil-types are independent results of the same primary factor of water distribution.

In sedentary hillside soils there may be a more direct effect of soil-type in that humus tends to retain more water and thus reduce drying-up through drainage; the heavier attacks found on soils with more humus might therefore be partly explained in this way.

Rainfall.

One would expect rainfall, through affecting the quantity of sap flowing up the trunks of the palms, to be a factor in distribution of *Melittomma*. Unfortunately in the Seychelles there is not a wide range of variation in precipitation, annual values in localities where records have been kept ranging between 1541 mm. and 2767 mm. In only one instance is there suggestive evidence of a rainfall effect.

Both east and west coasts of Conception Island are apparently similar, being precipitous, with many boulders in a soil of gritty loam. The only difference appeared to be in the rainfall, which is much heavier on the west or seaward coast; the infestation-rate here was 97 per cent. and the vast majority of the palms were very heavily attacked; on the much drier east face the rate was only 54 per cent., and individual palms were much more lightly infested.

In Madagascar, however, some strong evidence was obtained of rainfall as a limiting factor. The area studied was in the north-west, from the island of Nossi Bé and the Sambirano district northwards to Diego Suarez. Plantations were examined all along the route and sample counts of infested palms were made as in the Seychelles. *Melittomma* attack, while severe in Nossi Bé and the Sambirano district, was found to diminish on passing northwards, and northwards of Ambilobe as far as Diego Suarez none could be found. No explanation of this was apparent until rainfall figures were consulted; a close correlation could then be detected, as shown in Table VI. What appears to be more important than the annual rainfall, is the precipitation for the six-month dry period May–October, which falls in value much more conspicuously as one passes northwards. Plantations are more scattered towards the north, which might suggest that *Melittomma* has never reached those in the Diego area, but then there are many very small and equally scattered and isolated village plantations in the Sambirano area, which were all found to be attacked. There is no locality in the Seychelles with a dry season nearly as marked as in the north of Madagascar, the lowest figure for the driest six months at Anse Royale, which has one of the lowest recorded rainfalls, being in the neighbourhood of 500 mm.

TABLE VI.

Relation between rainfall and infestation-rate of *Melittomma insulare* in different districts of north-west Madagascar.

	District	Number of samples	Average infestation-rate (%)	Rainfall (in mm.)	
				Annual	6-month period May–October
↑ SOUTH	Nossi Bé and Nossi Comba	14	55	2250·7	338
	Sambirano	17	39	2146·4	242
NORTH ↓	Ambilobe	14	16	1859·6	85
	Diego Suarez	5	0	886·5	37

There is evidence that very dry conditions in the trunk may prove fatal for larvae. If blocks of wood in which larvae are kept are allowed to become too dry the larvae either die or fail to make any growth. One growing trunk which was dissected in Mahé was found to contain larvae several of which were either dead or moribund, the only apparent reason being the exceptional dryness of the wood due to some unknown cause. In the drier and harder wood of native palms there is evidence that many larvae never survive (p. 27). It would not therefore be surprising if a pronounced dry season is a limiting factor for the larvae of *Melittomma*, which spend not less than a year in this stage.

Drainage.

Unfortunately no attempt was made to correlate efficiency of drainage with the incidence of *Melittomma*. The alluvial soils round the marshes of the coastal plains are the only ones in which drainage can do much to alter the conditions of soil humidity, the high ground being mostly so precipitous that installation of drainage systems would be superfluous.

Age of the palm.

The wood of a coconut trunk is very much softer and more sappy when it is young (A.G. II and A.G. III). At this stage the base of the bole is much swollen, the vascular bundles are widely spaced and there is a large amount of parenchymatous tissue between them, so humid that fluid can readily be squeezed out of it (Pl. IV, fig. 2). In such wood the larvae of *Melittomma* find conditions most favourable, and grow more quickly and to a greater size. It is probable that a much greater proportion of a batch of larvae survive than in the drier wood of old coconut or of wild palms (Pl. IV, fig. 3), because the number of larvae found in younger palms is usually much greater.

During earlier studies of the pattern of infestations, and also later during examination of insecticide experiments, numbers of larvae in individual palms were estimated. In the majority of cases complete counts were made of all the larvae that could be found, but in some the number was computed by estimation, based on complete examination of, for example, one-half or two-thirds of the complete infestation. A comparison of the numbers in A.G. III and A.G. IV palms provides interesting data. Since the figures obtained for A.G. III palms in Mahé, where young palms are relatively few, are insufficient, only results from Praslin are recorded in Table VII. The results from examinations of healthy palms are kept separate from those from palms which had been treated with insecticide, since the treatments doubtless interfered to some extent with the results although the vast majority of larvae originally present were recovered. Although there is not much consistency in the results, it is evident that there are usually many more larvae in A.G. III palms, and more especially that the proportion of palms with large numbers (over 100) tends to be higher in this age-group.

TABLE VII.

A comparison of numbers of larvae in palms of age-group III and age-group IV in Praslin.

	Age-group III				Age-group IV			
	Number of palms examined	Range of numbers of larvae per palm	Average numbers of larvae per palm	Percentage of palms with over 100 larvae	Number of palms examined	Range of numbers of larvae per palm	Average numbers of larvae per palm	Percentage of palms with over 100 larvae
From dissections of healthy trunks	12	14–255	129·1	66·6	4	21–86	45·75	0
From examination of insecticide experiments	25	5–132	39·8	12·0	45	2–108	27·7	2·2
From both the above sources together	37	5–255	68·7	29·7	49	2–108	29·2	2·04

Since it is unlikely that a female would oviposit more freely, or lay more eggs in a batch, on the A.G. III palms, there is almost certainly a higher survival rate in the younger, more sappy trunks. Also as the larvae develop more quickly, and grow to a larger size resulting in bigger females which produce eggs in greater numbers, there is clearly a danger that in plantations with a high proportion of young palms the population of *Melittomma* will, after a number of generations, build up to a serious level very rapidly. The importance of fermentation of the wood, which not only does severe damage to the palm but may also greatly benefit the larvae, has already been pointed out; since sappy wood becomes fermented much more rapidly than drier wood, the threat to the welfare of the plantation will be readily apparent.

When this danger had been realised particular attention was paid to age-groups of infested palms, and to the relation of infestation-rates to the proportions of palms of each age-group in different plantations. In Praslin there are many coastal plantations with a high proportion of A.G. III palms. This exemplifies the results of a marked change in agricultural policy due to the slump years of the early 1930's; areas formerly under timber, rubber, vanilla etc. were turned over to coconuts, resulting often in solid areas of coconuts in which all the palms were planted together and have now been for a few years at an age when they are most susceptible to attack. Where conditions are suitable, numbers of *Melittomma* have in recent years built up to a peak, which has been largely responsible for the present alarm. A similar illustration was found in Silhouette, where a hillside area of 25 acres, formerly under rubber, was turned over to coconuts 30 years ago, and none of the palms are older than 25–30 years; the infestation-rate is now 66 per cent., which is high for a sedentary hillside soil, especially since it was badly eroded until measures were recently taken to stabilise it.

In Mahé the average age of palms is much higher than in Praslin as a rule, and there are few if any plantations composed entirely of young palms. A number were examined, however, which had strong admixtures of A.G. III palms with the older ones. Evidence from these was somewhat conflicting. In several localities at Cascade, and on Anonyme Island, for example, the younger palms were much more heavily infested than A.G. IV palms. At Police Point, Val Mer and Canelles, however, all in south Mahé, infestations were mostly in A.G. IV palms, younger ones rarely being attacked. The very heavily attacked plantation on the west coast of Conception (p. 37) consisted entirely of A.G. IV palms. The difference between Mahé and Praslin in this respect is shown by calculating the percentage of palms infested in each age-group from a random selection of several samples together (Table VIII). Palms of all age-groups are more frequently infested in Praslin, but A.G. III palms are infested relatively more frequently than A.G. IV palms. A.G. II palms have been included, but are not numerous enough to be significant.

TABLE VIII.

Comparison of extent of infestation in palms of different age-groups, in Mahé and in Praslin.

		Age-group II		Age-group III		Age-group IV	
		Infested	Not infested	Infested	Not infested	Infested	Not infested
Mahé	Total palms	6	24	86	154	278	563
	Percentage	20·0		36·0		33·5	
Praslin	Total palms	5	12	161	64	182	186
	Percentage	29·4		71·5		48·8	

One is led to conclude from the above evidence that although high concentrations of young palms are not always seriously attacked, yet those acute infestations which do occur are mostly in plantations consisting entirely or largely of A.G. III palms, and further, since they are more susceptible to damage, infestations in such plantations constitute a grave danger from the planter's point of view.

Associated vegetation.

Vesey-FitzGerald (1940, pp. 255–8) has previously enumerated many of the plants which are characteristic of different soil-types, and the lists of plants which were usually made in plantations sampled in the present work can add little to his statement.

As far as the herbaceous ground-vegetation is concerned, it was not observed to have any direct effect upon *Melittomma* distribution. It is possible that thick, unbroken mats of plants such as the grass *Stenotaphrum dimidiatum* (L.) Brongn. may rob the soil of so much water as to affect the flow of sap in the coconut palms, and indirectly the livelihood of the larvae. Investigation of this was not undertaken, but in any case such plant-growth is generally regarded as detrimental to the coconuts.

Large trees, however, such as "badamier (*Terminalia catappa* L.), "takamaka" (*Calophyllum inophyllum* L.), mango (*Mangifera indica* L.) and possibly *Casuarina* raise a different problem. The all too common practice of planting young coconuts beneath their shade may have serious results, not only on the health of the palms generally but also by drawing them up through shade-effect into tall trunks with soft, sappy wood, which is highly susceptible to *Melittomma* attack and to fermentation for reasons explained before. A good illustration was a hillside plantation near Scott Vale, Silhouette, which was still suffering from the shade effects of large *Albizzia* trees which had only recently been cut down. The rate of infestation was high for a hillside situation, although no sample-count was made.

To summarise the foregoing evidence on the humidity factor, it may be said that, in general, high concentrations of *Melittomma* occur where one or more environmental or other factors tend to produce a high level of humidity in the wood. This is not difficult to understand when the feeding habits of the larvae are taken into account.

Biotic factors.

The effect of the age of the tree is really a biotic factor which has already been discussed since it affects humidity.

It is sometimes asserted that *Melittomma* only attacks coconut palms of certain types. In the Seychelles about 90 per cent. of the palms are of the "coco seychellois" variety, but there are small numbers of other types, notably the Ceylon and Nicobar. These are both grown in some numbers together with the local form at Amitié (Praslin); sampling carried out for comparative purposes in the main part of the plantation was of no avail since *Melittomma* was either absent or very scarce. Isolated palms of Nicobar type in an adjacent area, however, were found to be infested, and palms of the Ceylon type were found infested in Victoria (Mahé). It therefore appears that any types likely to be important are subject to attack, although there is not enough evidence to judge whether one type is more subject than another; but this does not appear to be likely, and since for certain cultural reasons the indigenous type is more suitable for general cultivation in the Seychelles than either the Ceylon or Nicobar types, the matter is of no great importance as far as selection of types for planting is concerned.

There remains the question of associated insects and other larger organisms; most of these are secondary and depend upon *Melittomma* rather than influencing it; these will be dealt with later. There is one insect, however, which is frequently held to be a factor of some importance (Dupont, 1924), namely the large ant, *Odontomachus haematoda* (L.), which excavates its nests round the bases of coconut trunks, in the earth and in the rotten wood and cavities of older *Melittomma* infestations. Some planters contend that it protects a palm from attack, presumably by keeping ovipositing females away or destroying freshly hatched larvae, in much the same way as the ant *Oecophylla* protects coconut fruits from certain Coreid bugs. No such action has ever been witnessed, but in most of the sampling the presence or absence of *Odontomachus* has been recorded, so that it is possible to see to what extent the existence of *Odontomachus* is correlated with that of *Melittomma* in individual palms. The results are summarised in Table IX, in which all palms from a random selection of 10 samples are included. All these samples are from sedentary hillside soils with humus. Of the total 330 palms, 88 had colonies of *Odontomachus*. Of the 157 palms infested with *Melittomma*, one would expect $\frac{157 \times 88}{330} = 42$ approximately to be infested with *Odontomachus* also, if they are distributed at random, irrespective of its presence. There are actually 47 palms infested with both insects, which is not significantly different from the expected value; in fact it is somewhat greater, and not less, as one would expect if *Odontomachus* had any deterrent influence on *Melittomma*.

TABLE IX.

Summary of ten samples to illustrate the relation between occurrence of *Odontomachus haematoda* and *Melittomma insulare* in individual palms.

Number of sample	Palms with neither *Odontomachus* nor *Melittomma*	Palms with *Melittomma* only	Palms with *Odontomachus* only	Palms with *Odontomachus* and *Melittomma* both present
1	8	1	21	3
2	7	13	3	10
3	6	17	2	8
4	20	10	3	0
5	21	10	1	1
6	4	18	1	10
7	23	8	1	1
8	10	18	1	4
9	13	10	2	8
10	20	5	6	2
Total	132	110	41	47

Associated Organisms.

An account of micro-organisms and fungi associated with larvae of *Melittomma* has been given earlier (p. 13 *et seq.*). It remains to enumerate those animals, mainly macroscopic, which have been found loosely associated with the larvae. With the exception of one internal parasite they are all secondary, following behind the larvae in their progress through the trunk, and depending upon their initial activity in some way or other to a greater or lesser extent. For convenience they can be classified into four categories.

A. *Internal parasites.*

Only once was an internal parasite found; it was a Gregarine in the gut of a larva from Mahé (fig. 14). It did not appear to affect the health of the larva, and was not found again although looked for in many other larvae.

B. *Animals inhabiting wood in earlier stages of fermentation.*

COLEOPTERA.

Only two species of beetles and their larvae can be listed here.

(1) *Diocalandra frumenti* (F.) (CURCULIONIDAE). Larvae and adults sometimes bore into fermented wood, through which they make their own tunnels. They are by no means restricted to this habitat, and were bred on one occasion from the peduncles of inflorescences. In Madagascar, adults were found in borings, saturated with fermented exudation, at the openings of tunnels.

(2) *Xyleborus* spp. (SCOLYTIDAE). Beetles of this genus are abundant in the Seychelles, usually infesting wood which is unhealthy or necrotic from some cause, but they were never found in healthy, living wood of coconut or any other palm. Adults, larvae and pupae of *X. perforans* (Woll.) have been found tunnelling in humid fermented wood, and also in drier wood near the surface of a trunk infested with *Melittomma*. The same species was found in abundance in a recently fallen, dying coconut trunk, and in a standing trunk of *Albizzia* sp. which was dying after being ringed. *X. confusus* Eichh. was found in abundance in dry, discoloured wood in a coconut trunk of which the crown was dying, but which showed no sign of *Melittomma*.

C. *Animals inhabiting wood in later stages of rotting.*

A very long list of insects and other animals could be included here, and the following may be taken as a representative sample, including the most important. Most of them may be found also in any rotting wood or other vegetable matter, which they use as food, and are not restricted to wood which has rotted through the action of *Melittomma*. Others very probably only derive shelter from the crevices and hollows produced in the trunks.

In earlier stages of rotting, when the wood is brown and often rather wet, and has not yet disintegrated, the following have been found:—

ACARINA.

(1) *Histiostoma* sp. (ANOETIDAE).

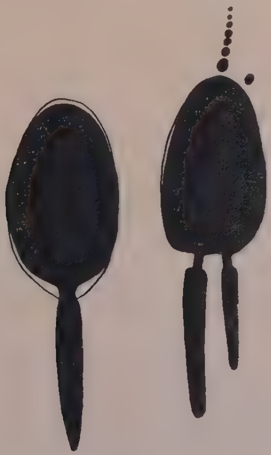


Fig. 14.—A gregarine parasite found in the gut of a larva of *M. insulare*.

COLEOPTERA.

(2) *Scydmaenus regularis* Schauf. (SCYDMAENIDAE).
(3) *Paromicrus atomus* Scott } (HYDROPHILIDAE).
(4) *Dactylosternum abdominale* (F.) }

The first three of these are very small and occurred on the walls of the larval tunnels. *Dactylosternum* is larger, and was only found once under particularly wet conditions.

In later stages, the wood becomes further blackened, and usually drier and more or less broken down into powdery detritus, the disintegration being accelerated by the activity of some of the animals themselves. The following have been recorded under these conditions.

Larvae of COLEOPTERA.

(5) *Oryctes monoceros* (Ol.) (DYNASTIDAE). Vesey-FitzGerald (1941) has given an account of the occurrence of this species, which is provided with an important breeding place through the activities of *Melittomma*.
(6) *Figulus striatus* (Ol.) (LUCANIDAE). The adults and larvae were found only once, in the hollow trunk of a *Stevensonia* palm.
(7) *Callirrhipis filiberti* Fairm. (RHIPICERIDAE).
(8) *Alaus mahenus* Fairm. (ELATERIDAE). A very large species.
(9) Genus near *Pyrophorus* (ELATERIDAE).

MYRIAPODA.

(10) *Scolopendra subspinipes subspinipes* Leach. A large centipede.
(11) *Iulomorpha* sp.

ORTHOPTERA.

(12) *Leucophaea surinamensis* (L.) (BLATTIDAE). Adults and nymphs, which are fossorial, are frequently found buried in detritus.

VERMES.

(13) Unidentified Annelids.

REPTILIA.

(14) *Typhlops braminus* (Daudin). A small snake, found in hollow trunks of coconut and *Stevensonia* palms in Mahé and Praslin.

D. *Animals living on outside of trunk or in roots, sometimes penetrating hollows inside the trunk.*

ISOPTERA.

(1) *Neotermes laticollis* (Holmgren). }
(2) *Nasutitermes mahéensis* (Holmgren). } TERMITIDAE.
(3) *Microcerotermes subtilis* (Wasm.). }

An account of the occurrence of these termites has been given by Vesey-FitzGerald (1941). They are not closely associated with *Melittomma*, and occur with equal frequency in palms and on islands which are not infested.

EMBIOPTERA.

(4) *Oligotoma scottiana* End.

DERMAPTERA.

(5) *Euborellia plebeja* (Dohrn.). Nymphs found on one occasion.

HYMENOPTERA, FORMICIDAE.

(6) *Odontomachus haematoda* (L.). The relationship between this and *Melittomma* has been discussed on p. 42, and also by Vesey-FitzGerald (1941).

(7) *Camponotus grandidieri* Forel. On rare occasions this ant replaces *Odontomachus*.

(8) *Camponotus maculatus* (F.). A large ant found in Madagascar in similar circumstances to the last two species.

Control Measures.

Historical.

The first mention of control measures in the literature is by Herscher and Millot (1911) in Madagascar, and by Dupont (1912) in the Seychelles. The early methods recommended were as follows:—

(1) Surgical treatment, by gouging (cutting out diseased wood containing larvae).
(2) Treating the trunks (either before or after gouging) with various poisons and deterrents (tar, lime, ashes, salt).
(3) Lighting fires at the base of the trunk or in hollows, to kill the larvae and harden the wood against further attack.
(4) Earthing and walling up, as a modified form of terracing and to keep the roots covered.
(5) Attracting adults to light.
(6) Certain preventive and sanitary methods.

Some of the more important of these merit more detailed attention.

Surgical treatment has been generally recommended and practised for 40 years or more (Herscher & Millot, 1911; Vuillet, 1913; Dupont, 1912–1938; Havard-Duclos, 1929; Vesey-FitzGerald, 1937, 1941; Frappa, 1948). It undoubtedly does some good, although too often it is carried out in an unskilled manner. It has to be remembered that larvae are not present in superficial rotten wood, but in the deeper "fermented" wood, which often appears more or less sound and is left in the trunk so that the larvae escape destruction; furthermore it is often too difficult and laborious to remove all the fermented wood in a deep infestation, and the operation may so weaken the palm that it will fall.

The surgical procedure therefore, for worth-while results, has to be combined with the application of poisons or other treatment to kill such larvae as may remain in the trunk. The use of tar has always been the most popular of these (Herscher & Millot, Vuillet, Dupont, Frappa etc.), and will be discussed in more detail later (p. 55). Lime has been used, and still is to some extent, but there is little evidence of any insecticidal effect since we have repeatedly found living larvae in treated palms; these remarks apply equally to the use of ashes. Salt was used in Madagascar by Mellis (Frappa, 1948), but since he required 40 lb. per palm, spread on the ground round the roots, it would not be practical or economical on the steep hillsides of the Seychelles, even if results are as good as he claimed.

Burning, although discouraged by Dupont (1912), has been widely practised, and the treatment still has its adherents; it will be discussed in more detail on p. 56.

Earthing up has been fairly widely practised, although not necessarily as a treatment for *Melittomma*. It was recommended by Dupont (1926), and a few years later (1932) he claimed some benefit from the treatment. Although earthing up by itself may have some protective effect against *Melittomma*, there is little doubt that it must be used in conjunction with insecticides for worth-while results; this will be discussed further on p. 54.

Preventive and sanitary measures, apart from the destruction of fallen palms (Dupont, 1914) were not greatly emphasised in early times. Certain precautions were recommended to avoid the growth of aerial adventitious roots, because it was thought that these encouraged oviposition; Dupont (1912) advocated keeping plantations free from weeds which are said to promote the growth of roots; Herscher and Millot (1911) and Vuillet (1913) stressed the avoidance of making wounds on the trunks, since these also stimulate root-formation. These measures, although beneficial, do not have as great an effect as was thought, however, since although females usually oviposit in crevices or among roots when available, these are by no means essential.

Dupont never ceased to advocate these measures for many years. Partly because they were not widely or efficiently carried out, and partly because they were largely ineffective, the situation did not improve, as he himself admitted (1938). Planters preferred to leave infested palms to their fate and replace them with young ones, which now often form up to about one-third of the total palms in a plantation, and grow up tender in the shade of older palms which produce a steady supply of adult *Melittomma* to infest them when they reach the susceptible age.

Vesey-FitzGerald (1937, 1939, 1941) made a critical summary of the merits of most of these early methods. He advocated the best of them, and was the first to make any concrete suggestions in the cultural and ecological field. He also advocated certain insecticide methods, but was unable to put them to a thorough test. Since then, the situation has remained much the same, and the reports of the Department of Agriculture of the Seychelles from 1945 to 1952 show no improvement in the extent of application of treatments or in results.

Objectives in control.

One must first have a clear idea, when approaching a control problem, of what one wishes to achieve. Total eradication of *Melittomma insulare* is a virtually impossible task; even if it were eradicated from coconuts, which would involve effective treatment, or destruction by fire, of over half the palms in infested islands, the native palms would remain as a reservoir containing small numbers. One must remember that it has been found in palms on the highest mountains of Silhouette. In any case, destruction of all infested coconut palms is undesirable, since it would take up to ten years to replant and raise fresh palms to the age of production,—a sacrifice which the colony could ill afford. It is therefore necessary to evaluate what measure of success can be achieved by less ambitious projects.

A survey of plantations with various degrees of infestation shows that if numbers of *Melittomma* are small the damage is not very serious, because individual palms do not often get attacked heavily, and stand a better chance of recuperation. A number of cases of chronic infestation may result, but even these palms may continue to produce good crops, especially if aided by cultural practices. It is only when infestation is heavy that major disaster results through extensive falling of palms; the damage is disproportionately greater as compared with the increase in numbers of the insects producing it.

It is therefore clear that a large measure of success could be achieved by keeping numbers down below a certain figure. This again offers some three or more possibilities between which it is far more difficult to choose:—

(1) To concentrate only on reducing the numbers in heavily infested areas and ignore other less heavily infested ones—a purely curative measure. This would involve full scale control first on Praslin, and in a few selected areas of Mahé, including some of its satellite islands such as Anonyme, Thérèse and Conception. Subsequent action would be to keep permanent watch on numbers and carry out full scale control operations where and as necessary.

(2) To attempt the much greater task of full scale treatment throughout all infested islands. This policy aims at reducing numbers everywhere to a level at which they are unlikely to become dangerous for many years, provided adequate vigilance is kept.

(3) To cover all infested islands, but to concentrate only on young palms (age-group II and III), leaving older ones on the grounds that many of them will be chronic, but would not live much longer or produce much more fruit even if treated, and in any case do not contain many larvae as a rule. These older palms should, however, be rigorously and drastically thinned out and replaced over a period of a few years, and careful watch should be kept on the younger palms, with constant re-treatment where necessary owing to the possibility of re-infestation from the older ones.

It is obvious that whichever of these policies is followed up, one can only expect to see conspicuous improvement in crop production after a period of several years. It remains now to consider the various methods of control which have been investigated.

Biological control.

The biological aspect has been the subject of special study by Dr. F. J. Simmonds, of the Commonwealth Institute of Biological Control; his report is to be published elsewhere.

Insecticidal control (fumigants and contact insecticides).

Until the present investigation, no insecticide has ever been given an extensive trial, if we exclude tar. Vesey-FitzGerald (1941) did some preliminary tests with cyanogas and paradichlorobenzene, and although he did not record any impressive results he made suggestions regarding methods of application which have formed the basis for our experiments. Apart from this, only sodium pentachlorophenate (Santobrite), and benzene hexachloride (Agrocide 7) have been tried, but only on a small scale, and no success was achieved (Milsum, 1949, 1950).

In choosing suitable insecticides for test, the habits and habitat of the larvae were taken into account. In view of their feeding behaviour, stomach poisons give little hope of success, except possibly systemic insecticides (to be dealt with later on p. 58). Considering the depth of the trunk at which they occur, contact insecticides would appear to have no better prospects, but for the fact that the larva is known to descend to the mouth of the tunnel at intervals to clear out the borings. Although the extreme hind end only protrudes from the tunnel, this offers a slight hope with an insecticide which can be applied so as to contaminate the tunnel openings. Deep infestations offer difficulties here, however, because larvae do not often descend into the rotten wood, and unless every trace of the latter is cleaned out before application (sometimes virtually impossible or so laborious as to be impracticable), many larvae will escape contact.

Fumigants therefore offer the best prospects, and the problem then arises of how to apply them. A preliminary test was carried out with aldrin, which is recognised as having a fumigant as well as a contact action, and which in the liquid form Aldrex could be sprayed on to superficial infestations and into cavities without preliminary gouging. The object was to see if any success could be obtained by the simplest possible method, but the results, in terms of dead larvae found when the trunk was dissected, were negligible.* Some form of enclosure to allow the fumigant time to diffuse into the tunnels was obviously necessary. Several variations of method were tried, and to cut a long story short the following procedure was evolved for superficial infestations (p. 22). The stages are illustrated on Plate VI and fig. 15.

---

* Further information about the effect of this treatment will be found on pp. 56–58.

(1) Sufficient surface wood is shaved off with a light axe or heavy knife (of the type usually known as a "panga") over the whole extent of the infestation, so as to cut across all the tunnels, which are thus freely opened up. It is unnecessary to remove all the fermented wood.

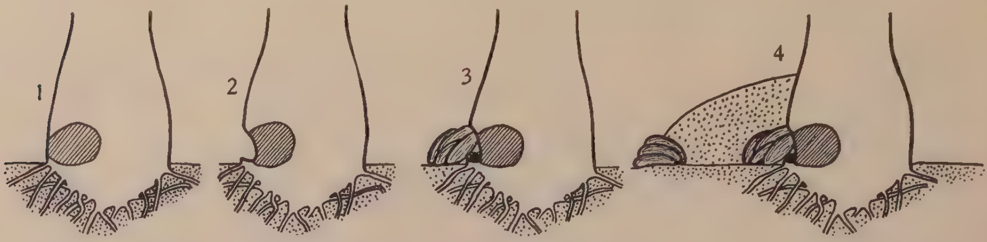


Fig. 15.—Stages in the fumigation treatment of a superficial infestation of *M. insulare.* 1, untreated; 2, a little fermented wood is gouged out from the surface; 3, paradichlorobenzene crystals are laid in the hollow, and coconut husks are tightly packed on to the top of it; 4, the husks are earthed over with soil, which may be held in position by an outer wall of husks.

(2) The insecticide is applied. If solid, it is spread out in the hollow formed, or dusted over the exposed surface. If liquid, it is sprayed on to the surface. In either case, it is advisable when opening up the infestation to cut little niches or shelves at the bottom to help contain the solid or catch trickles of liquid.

(3) Coconut husks are packed tightly into and over the hollow, to a level a little above the topmost tunnel openings.

(4) Soil is piled up and packed down tightly over the husks, to a level not less than a foot above them all over; the deeper the better.

A cavity is thus formed, filled with husks, under the soil. The husks do not prevent the insecticide from vapourising and the vapour from diffusing slowly into the tunnels. The importance of careful packing of the husks so as to form a firm, uninterrupted roof over the cavity cannot be too strongly emphasised, because any ingress of soil into the cavity may smother the insecticide, or the tunnel openings, or both, and thus obstruct the diffusion of the vapour into the tunnels.

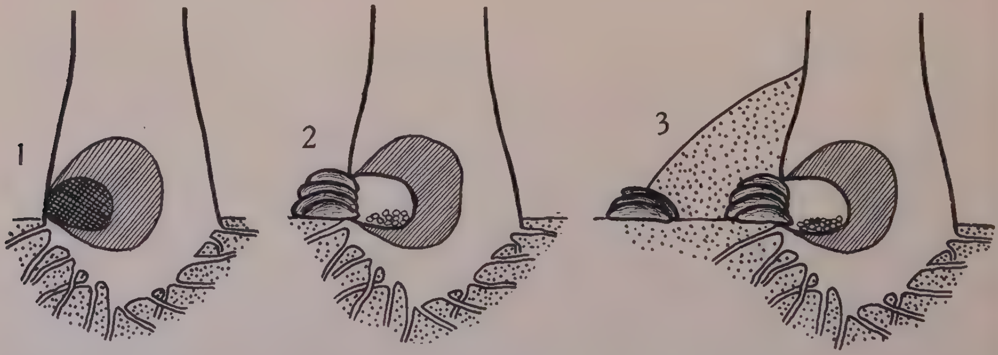


Fig. 16.—Stages in the fumigation treatment of a deep infestation of *M. insulare.* 1, untreated; 2, after gouging out all the rotten wood, and fully exposing the fermented wood in which the larvae are found, paradichlorobenzene is laid in the hollow and the entrance is closed by tightly packed coconut husks; 3, the husks are earthed over with soil.

For deep infestations (p. 22) the procedure is the same except that all rotted (as distinct from fermented) wood must first be removed from the infestation (fig. 16); a deep hollow is thus formed, which makes it impossible to work with an axe or knife, and gouges have to be used. The insecticide is spread or sprayed into the hollow, into the opening of which husks are tightly packed. The husks are then earthed over as before. Where rotting has extended far up inside the trunk the whole operation is awkward, and the chances of a successful treatment are not so good; one has then to consider whether the palm is worth saving or not; if not, it should be cut down and the trunk destroyed by fire.

The soil used in earthing up should be trodden down to render the fumigation cavity beneath as air-tight as possible. Loamy or sandy soil is the best, but clay may shrink away from the trunk when it dries and leave a gap through which vapour will escape. It should be piled high over the husks, having regard to the possibility of torrential rain washing some of it away. As we shall see, it is imperative that the earthing up should be maintained in good order throughout the time necessary for the insecticide to do its work.

Most of the earlier experimental work on insecticides was done at Grande Anse, Praslin. In March 1952, a limited number of infested palms were treated in the manner described above, using paradichlorobenzene (crystals), Aldrex, Dieldrex and Agrocide dispersible powder. The three last were applied in

TABLE X.

Results for earlier experiments with palms treated with paradichlorobenzene, Aldrex and Dieldrex, showing improvement of results with increase of time after treatment.

Insecticide and rate of application per palm	Time interval between treatment and examination (in days)	Total larvae obtained on dissecting trunk	Percentage of larvae dead when extracted from trunk
Paradichlorobenzene			
250 grams	5	206	50·0
250 ,,	9	37	12·0
250 ,,	55	32	52·4
250 ,,	68	13	100·0
250 ,,	69	25	100·0
250 ,,	69	8	100·0
125 ,,	72	15	20·0
250 ,,	72	36	25·0
250 ,,	83	99	99·0
250 ,,	84	46	91·3
250 ,,	86	23	64·7
250 ,,	88	119	95·0
250 ,,	89	22	100·0
250 ,,	89	84	98·8
Aldrex (10% emulsion)			
1000 cc.	54	56	77·0
1000 ,,	75	21	90·5
1000 ,,	83	106	91·0
1000 ,,	86	9	100·0
Dieldrex (10% emulsion)			
1000 cc.	83	88	95·45
1000 ,,	86	27	100·0

sprays with a stirrup pump; in some cases trunks were not earthed up after treatment. After a period varying between two and ten days some of the trunks were dissected and the larvae collected and examined. The results were very disappointing, both in trunks which had been earthed up and those which had not. The percentage of larvae killed in different palms varied between 11·4 and 54·3 per cent. Some of the palms which had been earthed up, however, showed a little more promise, and a number of those treated with paradichlorobenzene, Aldrex and Dieldrex were left for longer periods before examination,—up to two or three months. The results were then far better, and it became evident that an unexpectedly long time was necessary for the insecticides to produce the maximum effect. Table X, including the results from all the foregoing experiments in which palms were earthed up after treatment, shows this fairly clearly. Moreover, even after two months larvae were often found which had died very recently, while others were moribund and would probably have died later; and crystals of paradichlorobenzene or a strong smell of Aldrex or Dieldrex frequently remained. The poorer results with paradichlorobenzene (20, 25 and 64·7 per cent.) were instances of hollow trunks in which larvae were protected by a thickness of rotten wood which had been insufficiently cleared out. These results were good enough to encourage the conducting of experiments on a more extensive scale, both to see if sufficiently consistent results could be obtained to use the treatment as a standard method of control, and also to find out which insecticide gave the best performance; improvements in the detailed method of application would also be brought out.

Meanwhile certain other insecticides were tried out. Aldrin 20 per cent. wettable powder, and dieldrin 50 per cent. wettable powder were each applied to three palms by sprinkling the powder thoroughly over the whole gouged surface and in the hollow, and then packing in husks and earthing up in the usual way. Four of the palms (two under each treatment) were examined after two months, and the remaining two after three months. The percentages of larvae killed ranged from 0 to 66 in the case of aldrin, and 10 to 44 in the case of dieldrin. These results were so poor and inconsistent that these products were abandoned.

Benzene hexachloride was used in the earlier experiments in the form of Agrocide dispersible powder, sprayed on in aqueous suspension at strengths of 100 and 200 grams/gallon; the results were poor, 0 to 22 per cent. of larvae being found dead at periods up to 10 weeks after treatment. Gammalin liquid concentrate, on the other hand, which became available later, gave one or two promising results with small numbers of larvae, and it was decided to include it with the others in large-scale tests.

Large-scale experiment.—In all, 115 infested palms were treated. Thirty-seven of these were on Government property at Grande Anse, Mahé, and the remaining 78 on the property of Mr. Arthur Savy at Saint Sauveur, Praslin. Treatments were carried out between 8th October and 21st October 1952; the trunks were dissected and examined in the same order between 5th January and 28th January 1953, so that each palm was examined approximately three months after treatment.

The palms were selected at random, in the sense that all the infested palms in the areas selected were treated. Some were in the coastal plain, and some on hillsides, which at Saint Sauveur are very steep and rocky, so that a good range of conditions was experienced. Four palms only in the two areas were so difficult to treat as to render it impracticable. Six fell down after treatment and possibly in some cases as the result of it, so that actual results were obtained from 109 palms.

The insecticides used were paradichlorobenzene, Aldrex, Dieldrex and Gammalin, more palms being treated with paradichlorobenzene than with the others because it had given better results in the preliminary experiments and is more practical to use. Certain details concerning the quantities and mode of application were varied. With paradichlorobenzene, in the majority of cases 250 grams were used for each trunk, and this may be taken as a fair average; but superficial infestations of small extent require much less, and in extreme cases good results were obtained with 125 grams or even less than 100 grams; palms with deep infestations and hollows extending some distance into or round the trunk require more, and up to 375 grams were used on some occasions. Aldrex, Dieldrex and Gammalin are all emulsifiable concentrates containing respectively 24·4 per cent. of aldrin, 18·5 per cent. of dieldrin and 10 per cent. of γ BHC, and emulsions in water at the rate of 10 per cent. and 5 per cent. were used; the percentage strengths of the active chemicals were thus as follows: aldrin, 2·44 and 1·22; dieldrin, 1·85 and 0·925; γ BHC, 1 and 0·5. The diluted emulsions were sprayed on with a stirrup pump; the quantity used for each trunk had to be varied, as with paradichlorobenzene, according to the nature and extent of the infestation. It is rarely that a trunk can be adequately covered with less than 500 cc., and generally a litre is necessary. In most cases both of these quantities were tried on different palms, for each concentration of each insecticide.

Certain variations in method were used as controls, but these will be discussed later.

The results for the four insecticides in the large-scale test are summarised in Table XI. It will be seen that results are on the whole good; in 25 out of 37 palms treated with paradichlorobenzene every larva was killed, and in a further 6 over 90 per cent. were killed. In only three palms were inferior results obtained, but in these the failure was due to a deep, difficult infestation which had been insufficiently gouged out before treatment. The other three insecticides

TABLE XI.

Comparison of the performances of paradichlorobenzene, Aldrex, Dieldrex and Gammalin in large-scale experiment.

Insecticide		Percentage of larvae killed per palm									Total
		100	95–99	90–94	85–89	80–84	75–79	65–69	55–59	35–39	
Para-dichloro-benzene	Number of palms	25	3	3	2	1	—	1	1	1	37
	Percentage of palms	67·56	8·11	8·11	5·41	2·70	—	2·70	2·70	2·70	
Aldrex	Number of palms	14	5	1	2	1	1	—	—	—	24
	Percentage of palms	58·66	20·83	4·16	8·33	4·16	4·16	—	—	—	
Dieldrex	Number of palms	4	—	1	2	—	2	—	—	—	9
	Percentage of palms	44·44	—	11·11	22·22	—	22·22	—	—	—	
Gammalin	Number of palms	4	4	2	4	2	4	—	—	—	20
	Percentage of palms	20·00	20·00	10·00	20·00	10·00	20·00	—	—	—	

gave results which were rather less good, although there is not a great deal to choose between paradichlorobenzene and Aldrex. There is less consistency among the better results than in the case of paradichlorobenzene; this is brought out in a block-graph (fig. 17), which includes all those results showing a kill of over 75 per cent. The higher proportion of 100 per cent. kills with paradichlorobenzene is evident, the performances of the other three falling off in the order Aldrex, Dieldrex and Gammalin; in the last-named there are as many results of 75–80 per cent. as there are of 100 per cent. The total number of larvae killed in all palms together was as follows:—

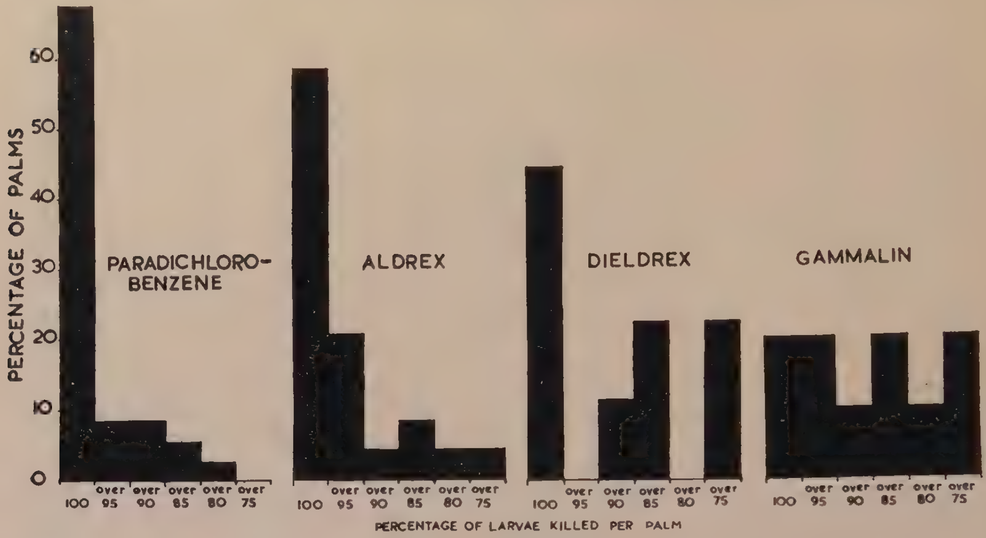


Fig. 17.—Block-graph comparing the better results achieved with the four principal insecticides. Note that paradichlorobenzene has produced a relatively greater number of 100 per cent. kills than the others; Aldrex comes next, while the other two are far less consistent.

	Total dead	Total living	% killed
Paradichlorobenzene	1065	49	95·60
Aldrex	466	31	93·76
Dieldrex	213	27	89·75
Gammalin	474	52	90·11

This brings out the merits of the four insecticides in the same order except for the last two, which are very similar.

The greater effectiveness of paradichlorobenzene is what one would expect, if one accepts that when applied to this problem in the manner described its action is wholly fumigant, whereas the other three insecticides have a greater contact than fumigant action. Contact action necessitates getting the substance in solid or liquid form on to each individual insect, which is clearly very difficult with larvae of *Melittomma insulare*; it involves exposing, in the preparatory process, every individual tunnel as far as that part of it which is frequented by the larvae some or all of the time, and this can seldom be guaranteed. This explains why concentration had little if any effect on the results with Aldrex, Dieldrex and Gammalin; good and poor results were obtained equally with 10 per cent. and 5 per cent. emulsions, and also no matter what volume was used provided the exposed surface was adequately covered, and it has not therefore been thought necessary to distinguish these in Table XI. It follows that even if higher concentrations of these three insecticides were used one could not expect significantly better results, and since at 10 per cent. concentration the expense is far greater than that of paradichlorobenzene, it is clear that the latter is both superior in performance and more economical, besides being more convenient to use under the difficult conditions on the steep hillsides.

The relative effectiveness of Aldrex, Dieldrex and Gammalin is far less easy to explain. In the experiments described aldrin (in the form of Aldrex) was much more consistently effective than γ BHC (in the form of Gammalin); since from the conditions of application one would suppose the fumigant action to be the more important, one would conclude that the fumigant action of aldrin is stronger than that of γ BHC. Hadaway and Barlow (1952), however, have shown that the fumigant effect of γ BHC is greater against mosquitos (*Aëdes aegypti* (L.)) than that of aldrin, when the vapourising surface was a mud block to which the insecticide had been applied in suspension. The discrepancy cannot be explained without further experiment, to show for instance whether the susceptibility of *Melittomma* larvae differs from that of mosquitos, or whether, when insecticides are sprayed on to *Melittomma* infestations in liquid form, there is in fact more contact action than we have supposed.

Pupae and adults are much less frequent in trunks than larvae, and so the evidence gained from experimental treatments was correspondingly less for these stages; what there was, however, is highly satisfactory, and is summarised in Table XII, which in addition to the large-scale experiment includes earlier results in which treatments were comparable. By a coincidence the vast majority of adults were in palms treated with paradichlorobenzene, and so no significant comparison can be made between the performances of the different insecticides. However, since all the adults were killed in palms treated with paradichlorobenzene, this is of no import. Pupae appear sometimes to escape destruction because they are often deep in the wood; but emergence occurs after a fortnight or less, and since the paradichlorobenzene may remain effective for several weeks it is clear that there is very little likelihood of any adults escaping from a properly treated palm.

TABLE XII.

Comparison of the numbers of pupae and adults of *Melittomma insulare* killed in trunks treated with paradichlorobenzene, Aldrex, Dieldrex and Gammalin.

		Paradichlorobenzene	Aldrex	Dieldrex	Gammalin
Pupae	Dead	12	—	3	—
	Alive	5	—	—	—
	% killed	70·59	—	100·0	—
Adults	Dead	27	3	1	1
	Alive	—	1	—	—
	% killed	100·0	75·0	100·0	100·0

Attention will now be turned to some variations of the treatment in the large-scale project, which were tried as controls and to bring out certain points which seemed important.

(i) Gouging.—Six palms were treated with paradichlorobenzene in the usual manner, except that no diseased wood was cut out first. The percentage of larvae killed was very irregular, ranging from 35·59 to 100, and averaging 67·48. Such unreliability testifies to the necessity of a thorough gouging out. This failure is due partly to the inability of the toxic vapours to get access to the larvae in the tunnels if these are not adequately exposed, and partly to the fact that one cannot see clearly, without gouging, the vertical and lateral extent of an infestation and where exactly to lay the insecticide and husks.

(ii) Earthing up.—The importance of correct earthing up cannot be overestimated. This was clearly shown on the steep hillside at Saint Sauveur, where in a few palms the earth fell away after treatment as a result of weather conditions or because it was not adequately walled up. Husks and insecticide were thus exposed to the air to varying extents, and vapours from the latter were lost. Results from these palms were poor, and were not included in the figures in Table XI. In seven palms the percentage of larvae killed ranged from 0 to 72·2, with an average of 33·3. This shows that earthing up must not only be done thoroughly, but must be maintained in good order throughout the two or three months necessary to kill the larvae. In the coastal plain or on relatively flat ground no trouble was encountered in this respect; a retaining wall for the soil is scarcely necessary, although a light wall of husks is beneficial (Pl. VI). The steep hillsides, on the other hand, create difficulties, and a substantial retaining wall is essential on the downhill side of the trunk. This may be as simple or elaborate as desired. In order to kill larvae, it has only to last about three months. But for the welfare of the palm it is advisable to make it as permanent as possible. Earthing up, as has been pointed out, encourages the growth of adventitious roots (Pl. V, fig. 7), which can help greatly in the recuperation of palms which have been severely attacked. If the earth is allowed to fall away these roots will dry up and perish, and a valuable asset will have been lost. Some planters, indeed, make a practice of walling up hillside palms whether attacked by *Melittomma* or not, as a modified form of terracing (Pl. VI, figs. 6 & 7). The increased production of such palms leaves one in no doubt as to the value of this practice. The building of permanent walls takes time, and may be found to slow up the progress of a large-scale insecticide treatment; in this case temporary walls may have to suffice for purposes of treatment, but planters would be well advised to replace them with permanent walls afterwards, or to provide labour sufficient to build them at the time of treatment.

It is sometimes claimed that earthing up alone will destroy larvae, without the necessity of an insecticide. Although this seemed unlikely, six palms were treated in the usual way, except that insecticide was omitted. Out of 117 larvae recovered from all palms together (they were not all examined exhaustively), only three were dead, and it is doubtful whether even these had been killed as the result of the treatment.

It is, however, asserted that repeated earthing up over a number of years is itself a protection against subsequent attack. This view is based largely on the mistaken idea that females require adventitious roots for oviposition, and these are covered by earthing up. There may, however, be some protective effect, but during the present investigation time was too short to put the matter to a thorough test. A careful watch was kept when examining palms which had been earthed up during treatments, to see whether young larvae had entered the trunk above the level of the earth. In one case it was found that they had, the larvae being only just under the surface and too young to have entered before the treatment was done. It has also been pointed out earlier that larvae may often enter healthy, normal bark some distance up the trunk. Such evidence as we have, therefore, indicates that it is by no means safe to rely on earthing up as a future protection.

(iii) Palms difficult or impossible to treat.—To judge from the large-scale treatment, when every infested palm in the areas concerned was treated when possible, about 4 per cent. of infested palms may prove virtually untreatable, and a further 5 per cent. of those treated may be expected to fall as a result of it. These may be regarded as a necessary sacrifice by the planter, but he should remember that they include those palms which are most likely to fall in any case during the next year or two, merely as the result of attack by *Melittomma*. At Saint Sauveur, 25 untreated palms were blown down in the adjacent area during the course of the experiments, mostly within one week, when the wind was strong.

Effect on associated micro-organisms.—Agar cultures were made on several occasions from fermented wood in trunks which had been treated with insecticides. The common rod form (type A, p. 14) was obtained after treatments with paradichlorobenzene, Aldrex, Dieldrex and Gammalin, and several of the other types, including yeasts, were also obtained after treatment with one or other of them. It is evident that the insecticides have little or no effect upon associated micro-organisms.

Comparison of paradichlorobenzene fumigation with historic methods.

Comparative tests have been carried out with the two principal historic control methods, namely tarring and burning.

(1) *Tarring*.—The method here is to cut and gouge out the surface wood from an infestation and then paint the exposure with tar. The larvae during their periodic descents to the openings of the tunnels then get a coating of tar and die. Many attempt to crawl right out, and die on the ground or hanging from the tunnel openings, but some crawl back and die inside the trunk. Three palms were treated by this method.

The first was examined after two days, when fresh borings were to be seen, chiefly between root-bases where the tar had not penetrated. The trunk was dissected and the following recovery made:—

Dead (tarred) larvae outside the trunk	84
,, ,, ,, inside the trunk	44
Living larvae inside the trunk	87
Living pupae ,, ,, ,, ...	2
Living adults ,, ,, ,, ...	2
Percentage of larvae killed	59·5

A second palm was treated most carefully, all rotten wood being removed more thoroughly than one could reasonably expect in large scale operations; this involved a great deal of time. Over a period of five days after treatment 200 larvae came out and were killed by the tar. After three weeks the palm was cut down and examined, and 35 dead and 50 living larvae were found inside. This gives a total of 285 larvae, 82·5 per cent. being killed.

A third palm was similarly treated, but instead of examining it after one treatment, the surface was re-tarred at intervals of a few days as shown below; the larvae which died on the outside were collected and counted after each repetition and estimated as a percentage of the total.

Date of tarring	Larvae killed outside tunnels
28.v.52	70 (30·2%)
17.vi.52	114 (44·9%)
20.viii.52	17 (7·3%)
23.viii.52	9 (3·9%)

The palms were then cut down and examined on 26.viii.52, when a further 20 dead and two living larvae were found inside, and two living adults. Thus even four separate tarring operations scarcely killed all the larvae, and the living adults would doubtless have escaped, since the tar dries up after a few days.

It is evident that tar treatment may yield some good results but is far from reliable, and the labour and time involved are considerable, especially with the repeated tarrings which are necessary for good results. Furthermore, the palms tested above had infestations of superficial type, which provide the best conditions for this treatment. With deep infestations it would be necessary to cut out rotten wood and tar the inside of the hollow formed, an operation which would be very awkward and much less effective since the exposed surface would be rough and tar would not penetrate easily into the smaller crevices. One of the most serious defects in the method, however, is its relative ineffectiveness against adults and pupae. The latter are deep in the wood and unaffected by the tar, and emerging adults have no difficulty in escaping after the tar has dried up.

It is sometimes held that tarring has an important preservative action on the wood and thus helps the palm to heal, but any such advantage is more than offset by its poor insecticidal performance. It does not help recuperation to the same extent as earthing up does, and has to be followed by earthing up for the best results.

There is one type of infestation, however, for which tar treatment is probably the best available; that is a superficial infestation in a wound so high up the trunk that the earthing up necessary for fumigation is impossible.

(2) *Burning.*—Many planters advocate burning round the base of a palm, or kindling a fire in the hollow after gouging out rotten wood, to kill the larvae, harden the wood and give it more resistance to further attack. A single experiment sufficed to prove the relative ineffectiveness of this procedure.

A hollow palm was selected, in which a thin shell only two or three inches thick remained round one half of the base of the trunk, the other half having rotted away to expose the central hollow. The larvae in the remaining shell were thus much more exposed to the action of fire than usual. Rotten wood was first thoroughly removed, and a fire was kept burning round the base for half-an-hour, involving the collection of coconut husks and fallen leaves for fuel from a considerable area round the palm. The next day, fresh borings had appeared and larvae could be heard biting when the trunk was struck. After three days another fire was kindled and maintained for a further half-an-hour, hot enough to singe some of the leaves in the crown. Two days later the trunk was dissected, and 37 living and 36 dead larvae were obtained, giving a percentage of 49·3 killed. The dead ones were those nearest the surface. Considering the ideal conditions for this method the result is poor. It is doubtful also if it does the palm any good.

On one or two occasions plantations were encountered in which vegetable refuse had recently been burned to clean up the property. Some of the trunks were charred on the outside, but still fresh borings continued to appear.

Taking into consideration the comparative difficulty and laborious nature of these historic practices, and the poor numerical results they give by comparison with those from paradichlorobenzene, there is no doubt that they are in every way inferior.

Insecticides as prophylactics.

Treatment of the outside of the trunk with an insecticide, with the object of defence against ovipositing females or the entry of young larvae would seem to hold some promise, although there are three factors which weigh against its application to this problem. These factors are:—

(1) Weather conditions are adverse, torrential rain being frequent during much of the year, and a combination of heat and humidity accelerating the decomposition of insecticides deposited on the outside of the trunk.

(2) Trunks would have to be protected all the year round, since the life-cycle is continuous and not seasonal; treatments repeated frequently enough to maintain prolonged protection might therefore prove laborious and expensive.

(3) Although it has not been proved, it is probable that females emerging in hollow trunks sometimes mate and oviposit *in situ* without leaving the palm. External treatment of the trunk would be of no avail against these adults.

There is thus much uncertainty about the prospects of control on these lines, and since the life-history is long and the rate of spread probably slow, it would need prolonged experiment over a period of not less than about five years to get significant results. A small-scale experiment was carried out, however, which provided enough information to justify a brief account.

Thirty infested palms in Mahé (20 at Canelles and 10 at Cascade) were sprayed all round the base and about 18 inches to two feet up the trunk, some with Aldrex and some with Dieldrex emulsions, at different strengths and intervals of time, as follows:—

Insecticide	Strength %	Time interval between sprayings (months)
Aldrex	10	1
		2
	5	1
		2
Dieldrex	10	1
	5	2

Five palms were subjected to each of these six treatments, 500 cc. of emulsion being used on each palm at each spraying. Once a month all the ejected borings (including cast tail-pieces) were collected and measured by volume for each palm. This was repeated also on the same dates for three "control" palms which were not given insecticide treatment.

The effect of treatment upon the volume of borings is interesting. At each collection an estimate was made of the rate at which borings had been cast out, in cubic centimetres per week, since the previous collection. There was considerable irregularity, as might be expected since no precautions were taken to safeguard against interference with the borings by animals and weather conditions.

Of palms treated with Aldrex, regular records were obtained for nine over a four-month period. The weekly rate of production of borings for all nine palms combined decreased from 20·9 cc. in August to 5·2 cc. in December, giving a drop of about 75 per cent.; three of these palms which had the maximum treatment (10 per cent. emulsion at monthly intervals) showed a combined decrease from 5·8 cc. to 1·4 cc., which is not greater than the overall value.

Of palms treated with Dieldrex, regular records were obtained for six over a seven-month period. The combined decrease was from 25·4 cc. per week in August to 16·0 cc. per week the following March, the decrease for two of the palms, which were under the maximum treatment, being from 18·0 cc. per week to 12·5 cc. per week; in both cases the decrease is by about one-third for the seven-month period.

For the three control palms the figures were very irregular, one showing a slight decrease, one a big increase and the third remaining the same; their combined output of borings rose from 10 cc. per week to 15 cc. per week over a seven-month period.

Inexact although they may be, these figures bring out some points of importance. Palms under a regular spray treatment with Aldrex or Dieldrex show a gradual decrease in the amount of borings cast out, which probably reflects a decrease in the number of larvae. For each insecticide, the extent of the decrease seems to bear no significant relation to the strength of the emulsion within the limits used. The decrease in the numbers of larvae could be explained in two ways: (1) by direct contact insecticidal effect upon the larvae;

(2) by preventive effect of the insecticide against subsequent infestation, so that larvae reaching the adult stage are not replaced.

Both of these factors may of course operate, but in fact the former is probably more important. The irregular and incomplete effects, irrespective of the concentration of the insecticide within the limits used, conform with this view, from what we know of the effect of contact insecticides (see p. 52). After six months of the Aldrex treatment four of the palms which were given the maximum aldrex treatment were cut down and examined. Living larvae were found in all, but in two of them some very small ones were found (about 7 mm. long) close to the surface, and in a third, larvae of about 10 mm. were found. In view of this, palms under other, less intense treatments were not examined in detail. It is fairly certain, in view of the small size of some of the larvae and their position near the surface, that they had entered the trunk since treatment began; that they were, in fact, less than six months old.

In another experiment at Grande Anse, Praslin, five palms were sprayed with 500 cc. of 10 per cent. Aldrex and five with 10 per cent. Dieldrex at rather irregular intervals over a period of nine months; dates of spraying were 1st April, 28th May, 25th June, 27th August, 19th October and 10th December. During all this time fresh dust and exuviae continued to be cast out from most of the trunks; the quantity decreased to a large extent, however, although it was not measured. On the following 4th February, nearly two months after the last spraying, three of the trunks treated with Aldrex were dissected, and all were found to contain small numbers of living larvae; some of these were about half-grown, but others quite small, down to 10 mm. long.

Whatever the nature of the action of periodic spraying with Aldrex and Dieldrex, it is clear that as a treatment it is far from satisfactory, even when applied at a frequency and concentration which on a large scale would be prohibitively expensive. As a prophylactic, it gives incomplete protection; as a direct killer, it leaves a high proportion of the larvae unaffected even after several months. Since aldrin and dieldrin are among the most effective and the most persistent insecticides, it is clear that prophylactic treatment holds very little promise unless something is done to render the insecticides used more durable and adhesive. Vanderplank (1953) has found that certain resins can greatly increase the durability of Dieldrex on coconut trunks, and experiments along these lines might yield results; but in view of the long life-history of *Melittomma* it would probably involve a very lengthy programme of research.

Systemic insecticides.

The knowledge that the larva feeds on fluid suggested that a systemic insecticide might be effective if it could be introduced in sufficient concentration into the sap stream, in spite of the fact that no success has hitherto been recorded with this type of poison against normal wood-boring insects.

Preliminary experiments were carried out with coloured dyes, to trace the course of the vascular stream in the trunk and thus show the best point at which to introduce a substance into it. Solutions of eosin or of red ink were used for this purpose. Two methods of introduction were tried: (a) through the roots, by watering an eosin solution on to the ground round the trunk to a radius of six feet; (b) direct into the trunk by means of a hole bored with a brace and bit. The latter was found to be the more successful method, and without going into details, it may be stated that fluid was found to pass both upwards and downwards from a hole bored about nine inches into the trunk of a healthy palm, and to spread laterally to some extent as it passed up or down, owing to a spiral course pursued by the vascular bundles, some of which travel round in a clockwise and some in an anti-clockwise spiral as they ascend in the trunk. In theory, one could therefore attack an insect in the trunk by introducing an insecticide into the sap stream either above or below it; usually, since *Melittomma* infestations are about at ground level, only the former is possible.

In the very few experiments carried out with systemic insecticides, holes about five or six inches deep, and ¾ inch in diameter, were bored into the trunk above the infestations, at about 18 inches above ground level. They were directed slightly downwards so that liquid would not run out. Either three or four holes were bored in each trunk, more or less equidistantly spaced round the circumference, but care was taken that a hole was bored above an infestation in such a position that the insecticide in passing downwards would spread to the right extent to permeate at least its central part.

Three systemic insecticides were used, each at two concentrations; each of six palms was given a different treatment as shown below:—

Insecticide	Quantity per hole (cc.)	No. of holes bored
Systox (50% O,O-diethyl O-2-(ethylmercapto)ethyl thiophosphate)	10	4
	2	4
Sytam (70% octamethyl pyrophosphoramide)	10	3
	2	3
BFPO (50% bis(dimethylamino) fluorophosphine oxide)	10	4
	2	4

The quantity of insecticide indicated was run into each hole from a burette, and water was added almost to fill the hole, which was then firmly closed with a wooden plug.

Fifteen days after treatment the palms were examined, all available larvae being dissected out. There were, unfortunately, very few, since in view of the highly poisonous nature of the insecticides palms had to be selected, in the interests of safety, in a remote place in the hills rather than one where larvae were abundant. However, such results as were obtained appear significant. The three palms given 10 cc. per hole were first examined. With Systox and BFPO there were five and three larvae respectively, all alive. In the trunk treated with Sytam only one (dead) larva was recovered, but the second palm treated with the lower concentration was therefore examined and yielded five living larvae. Thus out of 14 larvae only one was dead, although several were situated only three or four inches below the bore-holes. Conditions were, in fact, ideal for success, and the time factor is unlikely to be important here as with fumigants.

Failure is almost certainly due to one or both of two reasons. First, the larvae are always surrounded by necrotic wood, in which vascular conduction probably does not work. Secondly, although the larvae feed on fluid, they obtain it from parenchyma tissue and not direct from the sap stream. Dissolved insecticides may not diffuse out of the vascular bundles into the tissues, no matter whether the wood is healthy or necrotic. It is clear, at all events, that in many infestations there is a large volume of rotten wood below the majority of the larvae, which completely blocks the rise of sap or insecticides from the roots; and when introduced above them, the poison may run downwards only as far as the margin of the fermented wood.

The only other insecticide tested which could be classed as a systemic was parathion, which is however so weakly soluble that little can be conducted in the sap stream. A saturated aqueous solution was used, introduced into the trunk through bore-holes as before. The solution was fed into the holes from bottles with tubes, held in position for 12–24 hours so that the hole was always kept full. Five palms were treated at different times, and examined 4–8 weeks after treatment. Results were very inconsistent, the kill varying from 0–80 per cent.

It is clear from these few experiments that systemic insecticides are not likely to prove as effective as fumigants, and in addition, the difficulties of application and administrative problems involved by such dangerous poisons weigh heavily against their use.

Ecological control.

It is frequently found that insects attack the wood of living trees only when the health of the latter has been undermined by adverse conditions, either edaphic or biotic. Beetles may follow after previous attack by insects of other groups. The Lymexylonid, *Hylecoetus dermestoides* (L.), for example, is stated by Thomsen and others (1949) to penetrate the branches of beech only when it has been previously attacked by the Coccid, *Cryptococcus fagi* (Baer.); the fungus, *Nectria galligena* Bres., also plays a part, causing necrosis of the wood while the beetle larvae feed on ambrosia fungi growing on the walls of its tunnels. Munro (1926) forms the conclusion that bark-beetles are normally secondary to injurious agencies such as fire, drought and leaf-eating insects, which primarily weaken the host-trees.

Contrary to expectations, nothing of this kind was found in the case of *Melittomma insulare*. The ecological evidence given earlier indicates that the heaviest attacks of the beetle are usually in plantations of healthy palms, on soils which are favourable for coconut cultivation. It is true that micro-organisms are associated with the larvae, but they gain access with or after them, and there is never any reason to suppose that a palm is not in a perfectly healthy state when the larvae first enter the trunk.

This makes it difficult to suggest any ecological methods of control which have as their object the creation of conditions unfavourable to the beetle, because in many cases this will automatically produce an environment less favourable for coconuts. Similarly one cannot advise against coconut cultivation in types of environment where the beetle is most prevalent, because this would rule out much of the land where coconuts can be most profitable. There are, however, a few minor recommendations which can be made of measures which would contribute to the success of a large-scale insecticide operation without involving excessive labour or expense.

(1) *Coral sand soils.*—The coral sand of the coastal plains is exceptional, in that while it is highly favourable for coconuts, it evidently provides an environment less favoured by *Melittomma*, to judge from observed rates of infestation (Table IV). It is therefore important that coral sand soils should be exploited to the full for coconut cultivation, provided the soil is not too wet.

(2) *Marshes.*—Evidence has been given to show that *Melittomma* attack tends to be distinctly worse in narrow strips alongside marshes than in other parts of a plantation; the strip may often be as narrow as 10 or 20 yards. In extreme cases it would be beneficial to replace coconuts by other crops in such areas. There are a number of vegetable and other crops which would be suitable, but care would have to be taken that the absence of coconuts would not result in further encroachment of the marsh onto the drier areas.

(3) *Tuffes.*—Plantations on very dry, eroded hillsides produce tapered trunks and poor crops. The average numbers of nuts per palm in five of the worst plantations encountered were 2, 0·8, 0·7, 0·39 and 0·08. Coconut cultivation under these conditions is obviously unprofitable. Although *Melittomma* does not thrive in such plantations, palms sometimes contain enough larvae to act as an important reservoir from which neighbouring plantations may be re-infested. It is therefore important to do something about them, and fumigation treatment

without at the same time improving crop-production would be a waste of time and money.

Two alternatives therefore present themselves. (a) Coconut cultivation can be abandoned and the palms destroyed. (b) Fumigation treatment can be carried out, and the palms very thoroughly walled round and earthed up (Pl. VI, figs. 6 & 7) to improve their condition and raise production. If the latter alternative is adopted, each palm in the plantation must be carefully examined and evaluated before treatment, having regard to the fact that many palms on such hillsides have chronic infestations and hollow trunks. A policy of resolute destruction of the maximum number of infested palms should be pursued.

Cultural practices.

Some of the control measures advocated (but not widely applied) in the past are concerned with agricultural practice. The present work has thrown more light on some of these, and brought out one or two additional measures which, together with the ecological methods described above, would contribute in a small way to the success of large-scale control operations. The following recommendations can be made.

(1) Evidence has been given (pp. 38–41) to show that heavy concentrations of *Melittomma* build up in plantations consisting mostly or entirely of young palms about 15–25 years old. It is best therefore to avoid planting in such a way that all the palms in a plantation arrive at this age together. This may sometimes be unavoidable, but in any case it is of the utmost importance that palms should be very carefully watched when they are at the most vulnerable age. Treatment of an early, superficial infestation is not only much easier but more effective than treatment of an older one, and if it is carried out on a young palm there is a much better chance of complete recovery.

(2) Any practices which promote the growth of a soft, sappy trunk create conditions favourable to the larvae of *Melittomma*. Planting of coconuts among trees of other kinds may sometimes have this effect, especially if the coconuts are planted in the shade of an already well grown and closely spaced stand of other trees. If any other trees are incorporated into the same plantation with coconuts, then both palms and trees alike should be spaced out at the accepted distance necessary for successful coconut cultivation.

(3) Manurial treatment may be beneficial, like earthing up, in assisting the recuperation of a palm which has been attacked. There is, however, no evidence that such practices have any direct effect upon the beetle or its larvae.

(4) The custom of cutting steps in the trunks of palms to facilitate climbing them creates a danger, for not only does rot penetrate the wood through such wounds, but they sometimes form a point of entry for *Melittomma* larvae. This practice was particularly prevalent on the island of Nossi Bé (Madagascar) and in extreme cases every wound up to a considerable height showed signs of attack (Plate IV, fig. 4). In the Seychelles 20 feet was the highest point at which attack was found, and even this is exceptional. In one Madagascar plantation, in which 93 per cent. of palms had trunk wounds, 33 per cent. of palms were attacked through the wounds and only 9 per cent. through normal basal infestations. Cutting steps should at least be avoided within a few feet of ground level, where attacks mostly occur.

Prevention of spread.

We must consider under this heading two kinds of spread:—

(a) Extension of range within an island or plantation.

(b) Distribution from one island to another.

The risk of either can be reduced by a little legislation, which has in fact been supplied in the past but by no means always strictly complied with. Destruction by fire of the bases of the trunks of palms which have fallen owing to *Melittomma* attack is essential. It has been found that adult beetles may go on emerging from such trunks up to about three months after their fall. They should therefore be destroyed within a day or two after falling, and since they provide an important breeding place for *Oryctes* when the wood has rotted sufficiently, the whole trunk should eventually be destroyed; the splitting up and burning of the base, however, should be immediate.

With regard to the spread of the beetle from one island to another, all that can be done is to make sure that no coconut wood, nor the trunks of any palms, are transported from an island which is infested to one which is not. This will rule out the transport of larvae, and leaves only the possibility of a fertilised female adult gaining access to a boat which is sailing to an uninfested island. The likelihood of this happening is so remote that the legislation necessary to avoid it, which would be very extensive, would not be justified. Furthermore, when considering the question of transport by boat to other countries, one must remember that the adult female only lives three or four days.

Summary.

The biology of *Melittomma insulare* Fairm. (COLEOPTERA, LYMEXYLONIDAE), a wood-boring pest of coconuts in the Seychelles and northern Madagascar, has been studied from all angles, with the object of discovering practical means of control.

The stages in the life-history are figured and briefly discussed, supplementary details being given to the earlier accounts of Vesey-FitzGerald and others.

The feeding habits of the larvae are described in some detail, with particular reference to their association with micro-organisms which were almost invariably detected in infested wood surrounding the tunnels. The larva is shown to feed on fluid extracted from the parenchymatous tissues and not on solid wood.

The course of the development of an infestation in an individual trunk is described in detail, culminating in the fall of the palm. Variations in this process are correlated with the age of the palm and other factors. The spread of infestations through plantations and islands is also discussed. A detailed account is given of the symptoms shown by attacked palms, together with a critical revision of certain changes which have in the past been attributed to *Melittomma* attack.

An account is given of the occurrence of *M. insulare* in certain palms other than coconuts, in which it has been found.

The geographical and ecological distribution, and past history of *M. insulare* is discussed in the light of the feeding habits of the larva and other factors. It is shown that the highest rates of infestation are correlated with conditions of greatest humidity, and with the various edaphic and biotic factors which promote these conditions.

Organisms (other than micro-organisms) associated with *M. insulare* in the Seychelles are listed, and shown to be always secondary.

Control measures (other than biological control) are discussed and experiments connected with them are described. Attention has been given mainly to insecticidal methods.

It has been found that fumigation treatment is decidedly the most successful, while contact insecticides only occasionally produce good results. Of the fumigants, paradichlorobenzene has given results good enough to justify its use in a large-scale programme of control. Results from Aldrex (aldrin), Dieldrex (dieldrin) and Gammalin (BHC) are often good, but less reliable because their action is less fumigant and more contact. The reasons for this are discussed.

The mode of application of fumigants, involving preliminary preparation of the trunk and subsequent earthing up, is described.

The results of paradichlorobenzene treatment are compared with those obtained from the historic practices of tarring and burning the trunks, and are shown to be greatly superior.

Experiments involving the unsuccessful use of Aldrex and Dieldrex in a prophylactic capacity are briefly described.

Preliminary experiments with systemic insecticides offer little hope of success to compare with that of paradichlorobenzene.

Ecological control offers no prospects on a wide scale, but certain measures which can be applied locally can contribute towards the success of any large-scale programme of insecticide control. The same is true of certain cultural practices and legislative measures which may reduce the spread and help to prevent the build-up of strong local populations of the beetle.

Acknowledgements.

To do justice to all those to whom I am indebted for assistance in this work would be impossible, and I propose to mention only a few by name and must crave the indulgence of any who have been omitted.

To His Excellency the Governor of the Seychelles, Mr. F. Crawford, C.M.G., I owe much for his constant encouragement and interest in the work. To Dr. W. J. Hall, C.M.G., Director of the Commonwealth Institute of Entomology, I am indebted for advice and for keeping me supplied with the varied requirements for the work, in spite of the incredible difficulties of intercommunication with such remote islands. To Mr. F. Durocher Yvon, M.B.E., Director of Agriculture, and his staff for help and encouragement in all branches of the work; and especially to Mr. J. Dookley, whose cheerful and conscientious efforts as my assistant did much to make the work easier and pleasant. To Mr. D. Vesey-FitzGerald and Dr. F. J. Simmonds I am grateful for their co-operation in the earlier field-work; the former most generously gave up a part of his leave to accompany us during the first few months and gave us the benefit of his knowledge and experience not only of the problem in question but of agricultural conditions generally in the Seychelles; I have borrowed freely from his published work and unpublished report.

Mr. Cotton, of the Pathology Laboratory, kindly allowed me to use his laboratory and gave helpful advice in the course of microscopic and culture work on associated micro-organisms.

To the Director General of Agriculture, Madagascar, and members of his staff I am deeply grateful for making excellent arrangements for my work in Madagascar, and especially to Mons. L. Caresche, entomologist of the Service de la Défence des Cultures, who accompanied me personally during the whole of my tour.

Many friends among the planters of the Seychelles, too numerous to mention, through their kindness and hospitality and by giving me free scope to examine and experiment on their plantations, did a great deal to make the work smooth and agreeable.

For the identification of organisms listed on pp. 42–45 and elsewhere in this paper, I gratefully acknowledge the help of Dr. W. J. Hall, and of numerous specialists in the various groups:—Dr. S. P. Wiltshire of the Commonwealth Institute of Mycology (fungi); Sir Guy Marshall (Curculionidae); Mr. R. D. Pope and Mr. E. A. J. Duffy (Coleoptera); Dr. F. I. van Emden (larvae of Coleoptera); Mr. W. V. Harris (termites); Mr. W. D. Hincks (Dermaptera); Dr. V. M. Dirsh (cockroaches); Dr. E. S. Ross (Embioptera); Dr. H. W. Parker (reptiles); Mr. E. Browning (myriapods); Mr. G. E. J. Nixon (Hymenoptera). Dr. W J. Dowson kindly examined and commented on my preparations of micro-organisms, and identified them as far as possible.

References.

Barrett, O. W. & Mackie, D. B. (1912). Coconut Pests.—Philipp. agric. Rev., **5**, pp. 254–261.

Beeson, C. F. C. (1941). The ecology and control of the forest insects of India and the neighbouring countries.—1007 pp. Dehra Dun, the author.

Böving, A. G. & Craighead, F. C. (1931). An illustrated synopsis of the principal larval forms of the order Coleoptera.—Ent. Amer., **11**, pp. 1–351.

Bradley, J. T. (1940). The history of Seychelles.—2 vols. Victoria, Seychelles, Clarion Pr.

Brown, E. S. (1953). Rep. Dep. Agric. Seychelles, 1952, pp. 7–11.

Copeland, E. B. (1931). The coconut.—3rd edn. London, Macmillan.

Duffy, E. A. J. (1953). A monograph of the immature stages of British and imported timber beetles (Cerambycidae).—350 pp. London, Brit. Mus. (Nat. Hist.).

Dupont, P. R. (1912). Contribution à l'étude du cocotier aux Seychelles.—17 pp. Victoria, Govt. Print. Off.

Dupont, P. R. (1914). Rep. Agric. Seychelles, 1913, p. 17.

Dupont, P. R. (1917). *Ibid.*, 1916, p. 7.

Dupont, P. R. (1918). *Ibid.*, 1917, p. 20.

Dupont, P. R. (1920). *Ibid.*, 1919, pp. 10–11.

Dupont, P. R. (1924). Rep. Dep. Agric. Seychelles, 1923, p. 5.

Dupont, P. R. (1925). *Ibid.*, 1924, p. 5.

Dupont, P. R. (1926). *Ibid.*, 1925, p. 4.

Dupont, P. R. (1932). *Ibid.*, 1931, p. 11.

Dupont, P. R. (1938). L'archipel des Seychelles, ses ressources naturelles, sa faune entomologique et son évolution économique.—100 pp. Port Louis.

Durocher Yvon, F. (1949). Rep. Dep. Agric. Seychelles, 1947, p. 6.

Durocher Yvon, F. (1951). *Ibid.*, 1950, p. 9.

Durocher Yvon, F. (1952). *Ibid.*, 1951, p. 7.

Estève, J. R. (1925). Note sur quelques fibres textiles de la province d'Analalava. —Bull. écon. Madagascar, **21** (1924), no. 3–4 pp. 159–180.

Evans, J. W. (1952). The injurious insects of the British Commonwealth.—242 pp. London, Commonw. Inst. Ent.

Fairmaire, L. (1893). Bull. Soc. ent. Fr., p. cccxxiii.

Frappa, C. (1948). Un parasite du cocotier dans la région nord-ouest de Madagascar.—Agron. trop., Nogent, **3**, pp. 274–281.

Gahan, C. J. (1908). On the larvae of *Trictenotoma childreni* Gray, *Melittomma insulare* Fairmaire, and *Dascillus cervinus* Linn.—Trans. ent. Soc. Lond., **1908** pp. 275–282, pl. VI.

Gardner, J. C. M. (1937). Immature stages of Indian Coleoptera (22).—Indian For. Rec., **3**, pp. 127–140.

Hadaway, A. B. & Barlow, F. (1952). Studies on aqueous suspensions of insecticides. Part III. Factors affecting the persistence of some synthetic insecticides.—Bull. ent. Res., **43**, pp. 281–311.

Havard-Duclos, B. (1929). Le cocotier dans la province de Nossi-Bé.—Rev. Bot. appl., **9**, pp. 635–642.

Hendee, E. C. (1933). The association of the termites, *Kalotermes minor, Reticulitermes hesperus*, and *Zootermopsis angusticollis* with fungi.—Univ. Calif. Publ. Zool., **39**, pp. 111–133.

Hendee, E. C. (1935). The rôle of fungi in the diet of the common damp-wood termite, *Zootermopsis angusticollis*.—Hilgardia, **9**, pp. 499–525.

Herscher, G. & Millot, L. (1911). Contribution à l'étude du cocotier. Un nouvel ennemi: la " maladie " du cocotier (*Hylecoetus*).—Bull. écon. Madagascar, **11**, no. 1 pp. 41–49.

Hibbs, B. (1922). Rep. Agric. Seychelles, 1921, p, 3.

Hopkins, A. D. (1894). Notes on some discoveries and observations of the year in West Virginia.—Insect Life, **7**, pp. 145–151.

Lacordaire, J. T. (1830). Mémoire sur les habitudes des insectes coléoptères de l'Amérique méridionale.—Ann. Sci. nat., **20**, pp. 185–291.

Leach, J. G. (1940). Insect transmission of plant diseases.—615 pp. New York, McGraw-Hill.

Lepesme, P. & others. (1947). Les insectes des palmiers.—903 pp. Paris, P. Lechevalier.

Lionnet, J. F. G. (1952). Rendzina soils of coastal flats of the Seychelles.—J. Soil Sci., **3**, pp. 172–181, pl. I.

Lyne, F. S. (1923). Rep. Dep. Agric. Seychelles, 1922, p. 1.

Milsum, J. N. (1949). *Ibid.*, 1948, p. 6.

Milsum, J. N. (1950). *Ibid.*, 1949, p. 7.

Munro, J. W. (1926). British Bark-beetles.—Bull. For. Comm., Lond., no. 8, 77 pp.

Murray, A. (1867). List of Coleoptera received from Old Calabar, on the west coast of Africa.—Ann. Mag. nat. Hist., **20**, pp. 314–318.

Nichols, A. F. (1945). Rep. Dep. Agric. Seychelles, 1944, p. 2.

Pound, A. E. (1946). *Ibid.*, p. 5.

Pound, A. E. (1947). *Ibid.*, p. 5.

Riley, C. V. (1874). Sixth Annual Report on the noxious, beneficial and other insects of the State of Missouri, pp. 117–118.

Scott, H. (1926). Coleoptera from the Seychelles and adjacent islands.—Ann. Mag. nat. Hist. (9) **18**, pp. 50–76.

Squibbs, F. L. (1934). Rep. Dep. Agric. Seychelles, 1933, p. 7.

Thomsen, M., Buchwald, N. F. & Hauberg, P. A. (1949). Angreb af *Cryptococcus fagi, Nectria galligena* og andre parasiter paa bog i Danmark 1939–43.—Forstl. Forsøgsv. Danm., **18**, pp. 97–326, 43 pls.

Vanderplank, F. L. (1953). Causes of coconut nutfall and gumosis.—Nature, Lond., **172**, p. 315.

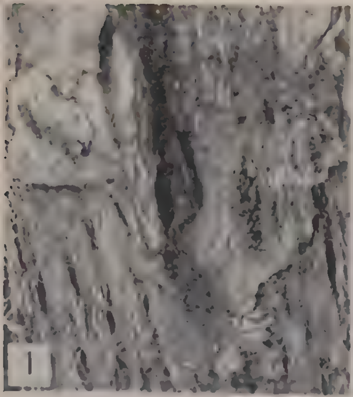
Vesey-FitzGerald, D. (1937). Rep. Dep. Agric. Seychelles, 1936, p. 18.

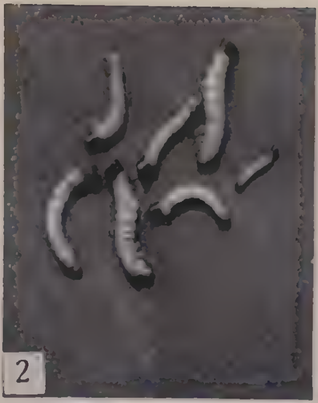
Vesey-FitzGerald, D. (1939). *Ibid.*, 1938, p. 16.

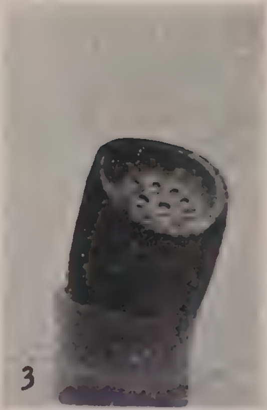
Vesey-FitzGerald, D. (1940). The control of Coccidae on coconuts in Seychelles.—Bull. ent. Res. **31**, pp. 253–283.

VESEY-FITZGERALD, D. (1941). *Melittomma insulare* Fairm. (Col., Lymexylonidae), a serious pest of coconut in the Seychelles.—Bull. ent. Res., **31,** pp. 383–402, 2 pls.

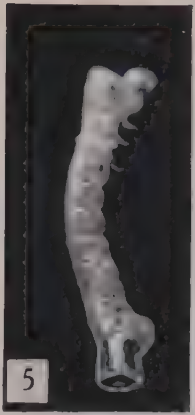
VUILLET, A. (1913). Deux ennemis du cocotier de la région malgache.—Agron. colon., **1,** pp. 33–36, 1 pl.

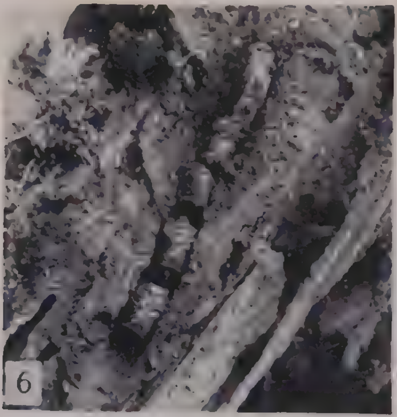

1

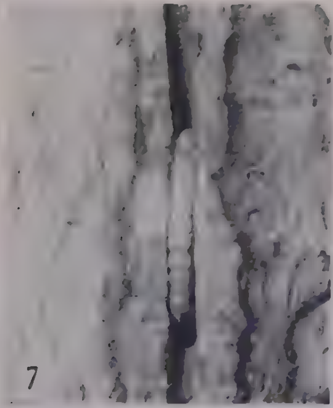

2

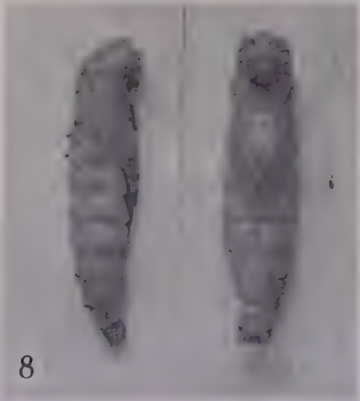

3

4


5


6


7


8

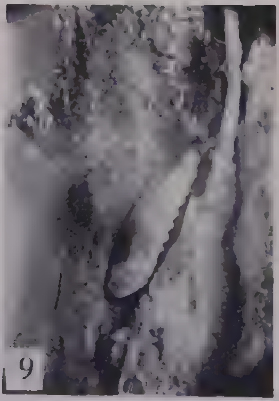
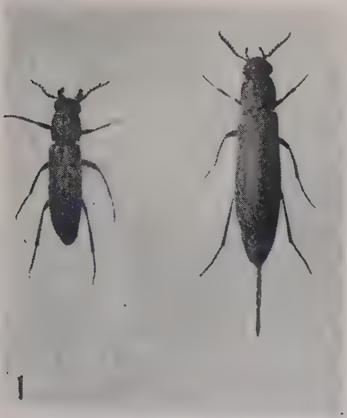
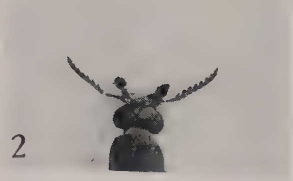
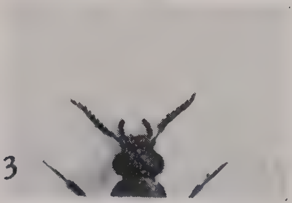
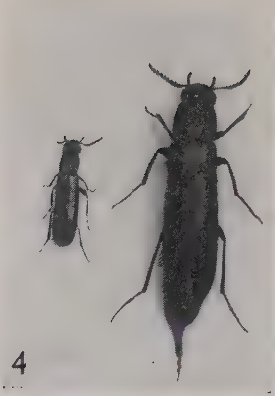

9

FIG. 1. Female *Melittomma insulare*, ovipositing in crevice on coconut trunk.
FIG. 2. Group of larvae of *Melittomma*.
FIG. 3. Posterior end of larva, much enlarged.
FIG. 4. Wood borings ejected from larval tunnel.
FIG. 5. Larva killed to show first thoracic and anal segments distended.
FIG. 6. Four successive exuviae from one larva, which has failed to eject them from the tunnel.
FIG. 7. Tunnel sectioned to reveal larva *in situ*.
FIG. 8. Pupa, enlarged; lateral and ventral aspects.
FIG. 9. Pupa *in situ*; note the cast " tail-pieces " above and below it.

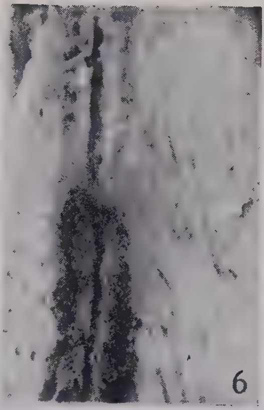

1

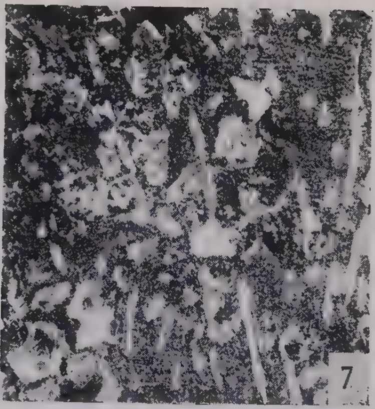

2

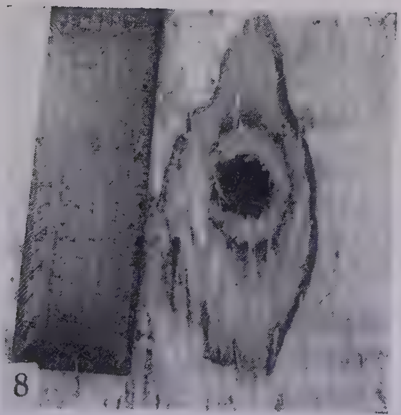

3


4

5


6


7


8

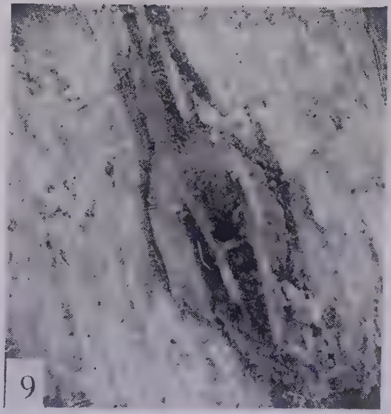
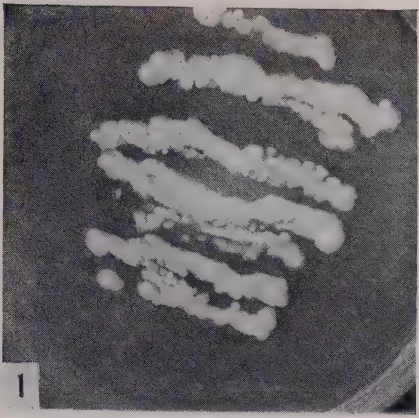
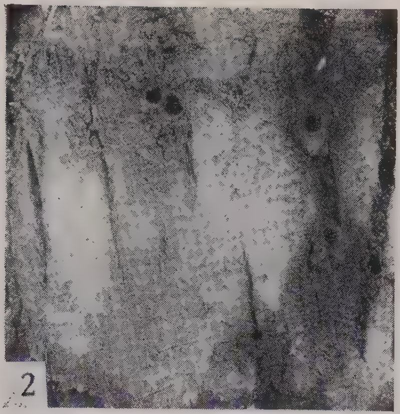

9

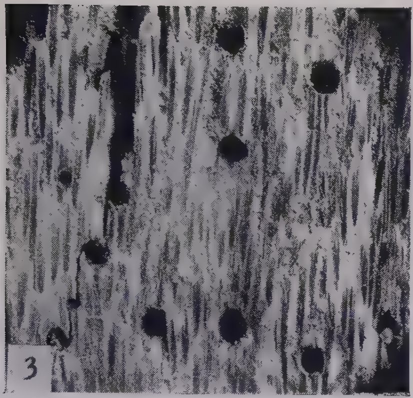
FIG. 1. Male (left) and female *Melittomma insulare*. (x 1·6).
FIGS. 2, 3. Head of male (above) and female (below), further enlarged.
FIG. 4. Smallest and largest females found. (x 1·7).
FIG. 5. Infested (" fermented ") wood showing larval tunnels cut transversely.
FIG. 6. Longitudinal section through larval tunnel in a wild palm.
FIG. 7. Old infested wood, showing larval tunnels invaded by fungal mycelium.
FIG. 8. Section through bore-hole in coconut trunk, after graft experiment.
FIG. 9. Section through bore-hole after injection experiment.



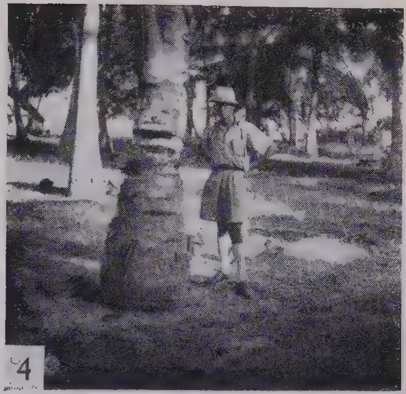
1



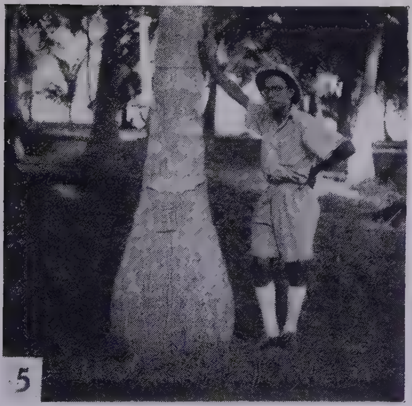
2



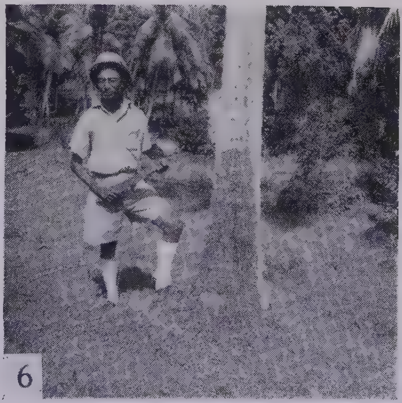
3



4

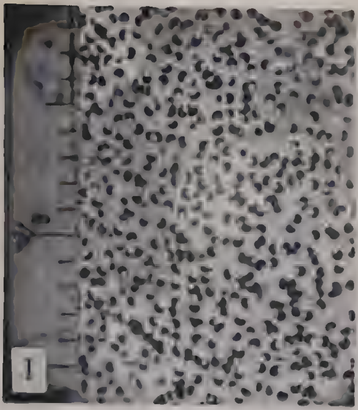


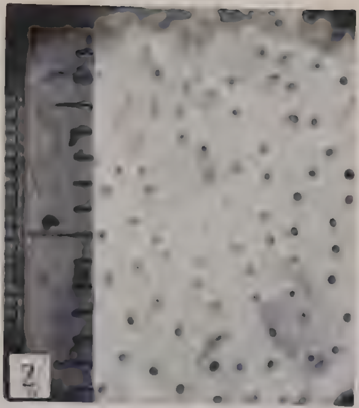
5

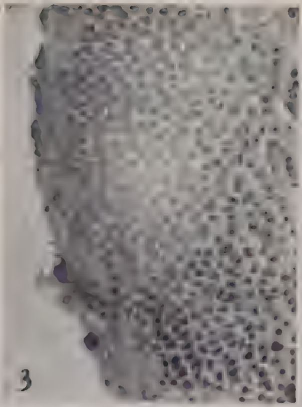


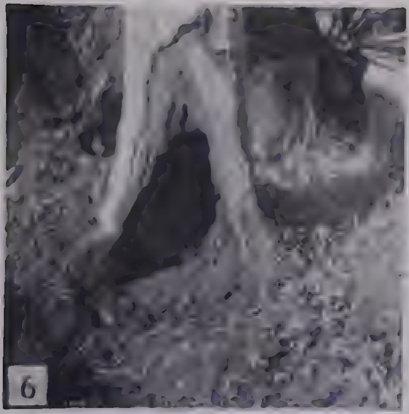
6

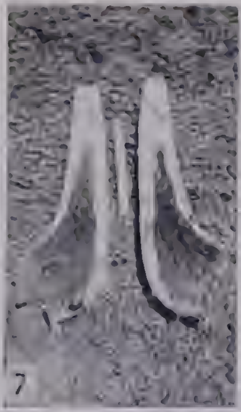
FIG. 1. Cultures on agar of micro-organisms from fermented wood.
FIG. 2. Entrances to larval tunnels in healthy coconut bark.
FIG. 3. Section of larval tunnels. Note that some pass through vascular bundles.
FIG. 4. Age-group II coconut palm.
FIG. 5. Age-group III coconut palm.
FIG. 6. Age-group IV coconut palm.

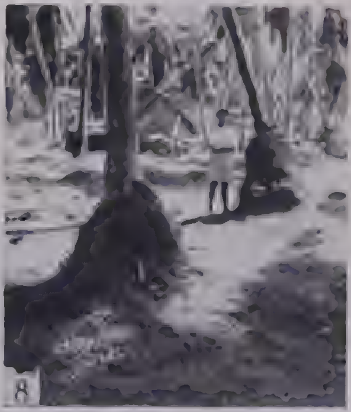




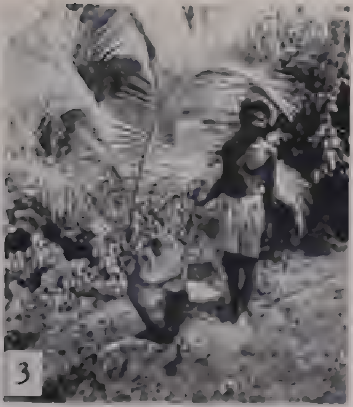


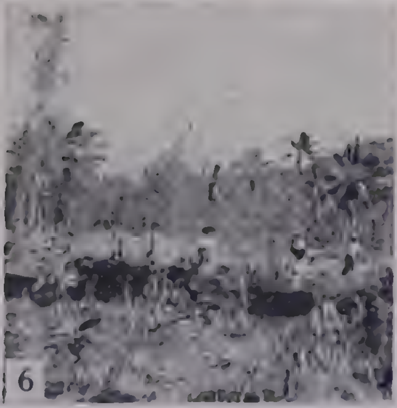


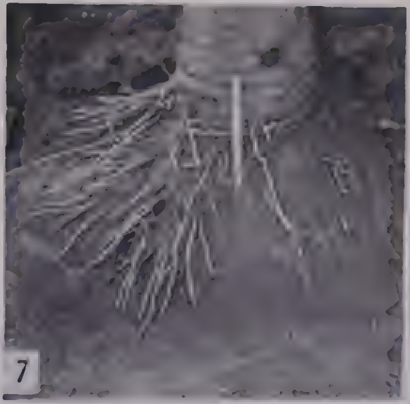




FIGS. 1-3. Transverse sections through palm wood. (1) Hard outer layer with concentrated vascular bundles, and (2) soft central wood, of coconut palm; (3) hard outer layer of *Stevensonia* palm.
FIG. 4. Infestations in trunk wounds, the highest pointed out by climber. Nossi Bé, Madagascar.
FIG. 5. Coconut palm fallen due to attack by *Melittomma*.
FIG. 6. " Hollow tree " stage of *Melittomma* attack in coconut trunk; the near wall of the hollow has been removed.
FIG. 7. The same stage in *Stevensonia* palm; trunk split in two.
FIG. 8. Coconut trunks with excessive growth of adventitious roots.







FIGS. 1, 2. Adjacent areas of the same plantation, showing different degrees of devastation on different soil types although the percentage of palms infested was almost identical: (1) On fertile loamy soil in valley; (2) on dry hill-face with laterite soil. This may be attributed to difference in recuperative powers (see pp. 44-45).

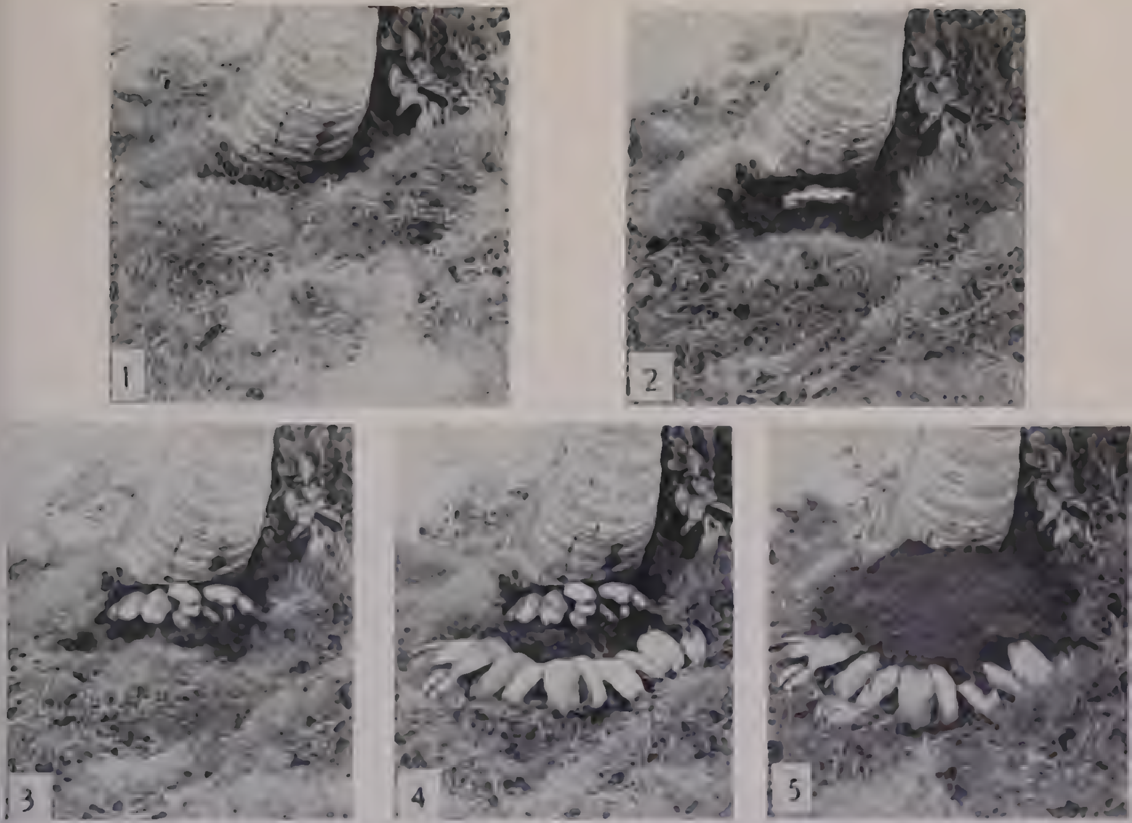
FIG. 3. Coconut palm of 25 years, showing extreme degree of " tapering " due to poor soil conditions.

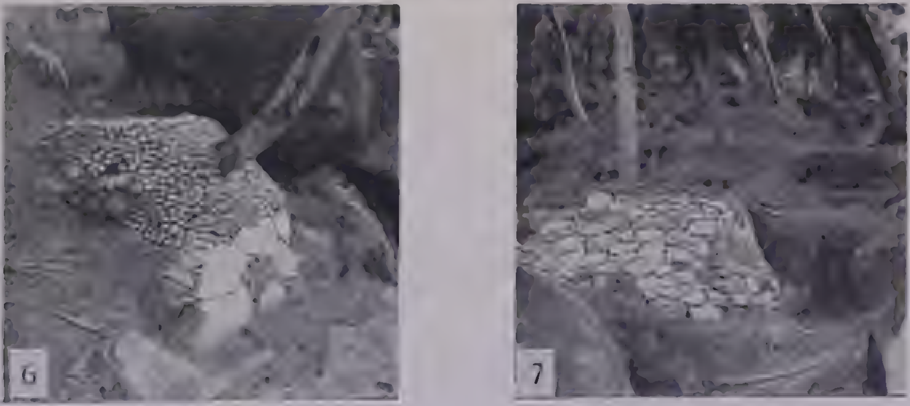
FIG. 4. Impoverished coconut plantation on poor hill-side soil. (The ground only appears flat due to tilting of the camera).

FIG. 5. Coconut palm dying in the crown; a condition often attributed, but not always rightly, to *Melittomma* attack.

FIG. 6. Coconut plantation in coastal flat, seriously impoverished by prolonged *Melittomma* attack.

FIG. 7. Coconut trunk after earthing up and removal of earth several weeks later. Note the growth of adventitious roots encouraged by the soil.





Figs. 1-5. Fumigation of infested coconut trunk with paradichlorobenzene. (1) Untreated; (2) surface wood gouged away and insecticide (white) laid in position; (3) husks are packed over the insecticide; (4) a wall of husks is laid on the ground at a little distance from the trunk; (5) earth is piled up over the husks.
Figs. 6-7. Elaborate walling up operations which are sometimes carried out on steep hill-sides, using stones and coconut husks.

STUDIES ON THE RESPONSES OF THE FEMALE *AËDES* MOSQUITO.

PART VI.—THE ATTRACTIVENESS OF COLOURED CLOTHS TO CANADIAN SPECIES.

By A. W. A. Brown.

Professor of Zoology, University of Western Ontario, London, Ontario.

The purpose of this study was two-fold; to evaluate the attractiveness to the northern Canadian mosquitos of fabrics worn by the armed services; and to investigate the physical principles determining the attractiveness of coloured surfaces to these insects. The project was an extension of studies already undertaken in 1950 with coloured cloths placed on robots or "dummy men" (Brown, 1951).

Observations on the colour preferences originally made with *Aëdes aegypti* (L.) (Brett, 1938) had been extended to cover several western American species of *Aëdes* (Gjullin, 1947). The latter author tentatively concluded that colours are chosen on the basis of their spectral reflectance rather than by any colour discrimination by the mosquitos. The experiments in 1950 on the northern Canadian species showed that the attractiveness was less with the lighter shades and luminescent varieties of colours (Brown, 1951). In the 1951 studies here reported an opportunity was given to correlate the attractiveness of different coloured cloths with their percentage reflectance of light in the visible and ultra-violet ranges.

Materials.

A total of 32 different cloths, each measuring 2 ft. by 4 ft., were compared for their attractiveness to mosquitos. They consisted of eight woollen flannels, dyed to Munsell standard colours (Nickerson, 1948) by the Ontario Research Foundation, Toronto; four satins, from Canadian Celanese, Drummondville, Quebec; three fluorescent satins, from the Guarantee Silk and Dye Company, St. Catherines, Ontario; 17 Service cloths, comprising five nylon canvases, three cotton drills, two worsted serges and seven miscellaneous cloths.

The robots, on which the cloths were tested, were assembled and operated according to the method described in a previous paper (Brown, 1951). They were maintained at a water temperature of 98°F., and were clothed in a felt undershirt.

The locale was Goose Bay, Labrador, in the vicinity of the U.S. Pumphouse Creek. At the time of the experiments, which were carried out between 4th and 21st July 1951, the species of mosquitos involved were *Aëdes punctor* (Kirby), *A. pionips* Dyar, *A. communis* (DeG.) and *A. fitchi* (F. & Y.).

Method.

The 32 cloths were divided into four groups of eight cloths each, and comparisons were first made between the eight cloths in each group. Group I comprised the eight Munsell flannels, and Group II included the four satins, the three fluorescent satins, and one black crêpe. Groups III and IV were made up of 16 Service cloths.

In the first series of experiments, comparisons were made between pairs of cloths, one on each robot. After a 10-minute wait, four counts of landing-rates for two-minute periods were made on each side of each robot, making a total of eight paired counts and 16 minutes of observation (see Brown, 1951). In order that any given cloth might be compared with the seven others in the group, it was necessary to make a total of 28 comparisons for the entire group. Cloths in Groups I and II were compared in this way.

In the second series of experiments, comparisons were made between all eight cloths in a group, and finally between the two best cloths of each group, upon army personnel. Four men in khaki drill knelt facing each other at the corners of a square of 6 ft. side, and the cloths were draped round the small of the back. An observer was assigned to each man, and the landing rates of mosquitos on an area measuring 24 ins. long by 14 ins. wide were counted for a one-minute period. Each group of eight cloths was rotated around the four men, so that any one cloth was successively worn by each of the four men. Every count was made after a one-minute waiting period. Finally a group of eight cloths, comprising the two most attractive of each of the four groups, was similarly rotated so that a common basis of comparison could be found for all 32 cloths.

In the third series of experiments, the four groups of cloths were similarly rotated on the two robots instead of the four men. Three rotations were employed for each group; in the second rotation the order of the cloths was reversed, and in the third they were shuffled; thus each cloth was assessed three times. Landing rates were counted for a period of two minutes each time following a wait of 1·5 minutes. The two best cloths of each of the four groups were similarly compared in a final group.

The reflectances of the cloths in the visible range of the spectrum were measured on a General Electric recording spectrophotometer with a 10-mμ slit, the surface of reference being magnesium oxide deposited from burning magnesium. A working standard of V3-G7 *Vitrolite* glass was employed to correct for specularly reflected light. The reflectances in the ultra-violet range were made according to the absolute method (Taylor, 1920) with more recent refinements, using a magnesium oxide standard. The reflectances obtained by the two methods overlapped in the 400–426-mμ range, and the slight discrepancies in the figures were smoothed off arbitrarily.

TABLE I.

Attractiveness to *Aëdes* mosquitos of cloths worn by robots; paired experiments with Group I flannels.

	Dark red	Dark blue	Light red	Purple	Light blue	Dark green	Yellow	Light green
Dark red ..	x	13	30	22	8	25	2	7
Dark blue ..	87	x	33	32	28	41	22	53
Light red ..	70	67	x	40	80	15	24	16
Purple	78	68	60	x	32	48	45	6
Light blue ..	92	72	20	68	x	80	27	10
Dark green ..	75	59	85	52	20	x	33	57
Yellow	98	78	76	55	73	67	x	50
Light green ..	93	47	84	94	90	43	50	x
Totals ..	593	404	388	363	331	319	203	199

The figures are the percentages of the total landing rates on the pair of colours tested.

Results.

The attractiveness of the variously coloured Munsell flannels and the satins, when compared in pairs, is summarised in Tables I and II. The values given for each colour are the percentages of the total landing rate on the pair of colours. For example, in the comparison of dark red with dark blue Munsell flannel, as shown in the top left-hand corner of Table I, the figures of 13 under dark blue on the top line and of 87 under dark red on the second line are the percentages represented by a landing rate of 7 and 47 respectively. The percentages obtained by each colour against the other seven colours are totalled at the bottom of the Table. It will be seen that among the flannels, dark red was the most attractive, followed by dark blue, light red and purple. In the case of the satins (Table II), dark red and dark blue were the most attractive, being exceeded only by the black crêpe.

TABLE II.

Attractiveness to *Aëdes* mosquitos of cloths worn by robots; paired experiments with Group II satins.

	Black crêpe	Dark red	Dark blue	Dark green	Lumin. red	Lumin. green	White satin	Lumin. yellow
Black crêpe ..	x	40	31	27	18	31	22	2
Dark red ..	60	x	38	28	30	47	38	3
Dark blue ..	69	62	x	28	40	43	42	12
Dark green ..	73	72	72	x	54	16	18	23
Lumin. red ..	82	70	60	46	x	35	48	9
Lumin. green ..	69	53	57	84	65	x	56	0
White satin ..	78	62	58	82	52	44	x	8
Lumin. yellow ..	98	97	88	77	91	100	92	x
Totals ..	529	456	404	372	350	316	316	57

The figures are the percentages of the total landing rates on the pair of colours tested.

The landing rates obtained by the four series of cloths when worn by army personnel are shown in Table III. It will be seen that dark red and purple were the most attractive of the flannels, and dark blue and dark red * the most attractive of the satins. In Group III navy blue serge and black drill, and in Group IV the tropical suiting and black-filled nylon, were the most attractive. When these were compared in a fifth or "playoff" group, the black cotton drill, the dark red Munsell flannel and the navy blue serge were the most attractive of all.

In deriving an attractiveness rating which could be applied to all the cloths, black cotton drill and navy blue serge were assigned the value of 100, and the ratings of all the others were expressed as a percentage of it. These two cloths were considered as equally the most attractive, because the serge was superior in Group III while the drill was equally superior in Group V. When assessed among the cloths of Group III they had a total landing rate of 133 + 155 = 288 (see Table III). Therefore if the remaining six cloths of this group are to be ascribed attractiveness ratings comparable to 100 for black drill and navy blue serge, their landing rates must be multiplied by 200 and divided by 288.

---

* The superiority of dark red to luminescent red, not shown by these figures, is amply confirmed by the results reported in Tables II and IV.

TABLE III.

Landing rates of *Aëdes* mosquitos on cloths worn by army personnel (rotation experiment).

Group I		Group II		Group III		Group IV		Group V	
Dark red	67	Dark blue	39	N. blue serge	155	Tropical suit	82	Black drill	72
Purple	56	Dark red	26	Black drill	133	Black-f. nylon	62	Dark red (I)	64
Light red	45	Lumin. red	29	AF blue serge	91	Khaki flannel	54	N. blue serge	60
Light blue	29	Black crêpe	25	Black, not m.	89	Perfection drill	53	Purple (I)	54
Dark blue	28	Dark green	22	Blue nylon	88	Tentage	46	Tropical suit	36
Yellow	21	White	15	Blue rayon	81	Brown nylon	32	Dark red (II)	34
Light green	18	Lumin. green	9	Black, mercer.	77	Green nylon	21	Black-f. nylon	33
Dark green	15	Lumin. yellow	2	White drill	62	Olive nylon	16	Dark blue (II)	26

The other groups are brought up to the basis of Group IV by utilising the comparative figures in Group V. For example, the dark red and purple flannels of Group I had a total landing rate of 64 + 54 = 118 as compared with 72 + 60 = 132 for black drill and navy blue serge, when all four were tested in Group V (Table III). Therefore the attractiveness value of dark red and purple flannels, taken as a pair, compared with that of black drill and navy blue serge at 100, is 118/132 × 100 = 89. Since the relative attractiveness of these two colours *vis-à-vis* each other was 54 : 46 (based on the relative figures of 64 to 54 in Group V, as well as the relative figures of 67 to 56 in Group I, each showing the ratio of 54 : 46, which was taken as the average ratio), the attractiveness value of dark red was set at 96 (89 + 7) and that of purple was correspondingly set at 82 (89 − 7). Similarly the leading pair of Group II had an attractiveness value of 45, compared with black drill and navy blue serge at 100 in Group V, apportioned on the basis of the average of their relative attractiveness (51·5 : 48·5) in Groups II and V, between dark blue (46) and dark red (44) satin. The leading pair of Group IV had an attractiveness value of 52, compared with black drill and navy blue serge at 100 in Group V, apportioned on the basis of the average of their relative attractiveness (45·5 : 54·5) in Groups IV and V, between the tropical (57) and the black-filled nylon (47).

The attractiveness ratings for the remaining six cloths in each of the four groups now require determination. In the Group I series, for example, the dark red and the purple flannels between them amassed a landing rate of 67 + 56 = 123; this is to be compared with their attractiveness value, based on Group V results, of 96 + 82 = 178. Therefore in order to obtain the attractiveness ratings of the other cloths in Group I, their landing rates must be multiplied by 178/123. Similarly those in Group II must be multiplied by 90/65, and Group IV by 104/144.

The landing rates obtained by the four series of cloths when worn by the robots are shown in Table IV. Dark red and dark blue flannel were the most attractive in Group I, and black crêpe and dark red satin were the most attractive in Group II. In Groups III and IV, black drill, navy blue serge, khaki flannel and the tropical suiting were the most attractive. When all the cloths of the fifth group were compared as before, the black drill, the navy blue serge and the dark red Munsell flannel proved to be the most attractive.

TABLE IV.

Landing rates of *Aëdes* mosquitos on cloths worn by robots (rotation experiment).

Group I		Group II		Group III		Group IV		Group V	
Dark red	57	Black crêpe	59	Black drill	63	Khaki flannel	113	Black drill	178
Dark blue	35	Dark red	37	N. blue serge	53	Tropical suit	85	N. blue serge	160
Purple	32	Lumin. red	36	AF blue serge	30	Tentage	72	Dark red (I)	146
Light blue	32	White	36	Black, not m.	27	Black-f. nylon	71	Dark blue (II)	88
Light red	32	Dark green	34	Black, mercer.	20	Brown nylon	52	Purple (I)	61
Yellow	10	Dark blue	25	Blue nylon/ rayon	20	Perfection drill	48	Tropical suit	58
Dark green	7	Lumin. green	22	Blue nylon canvas	18	Green nylon	19	Dark red (II)	49
Light green	6	Lumin. yellow	9	White drill	9	Olive nylon	14	Black-f. nylon	39

Black drill was more attractive than navy blue serge both in Group III (63 : 53) and in Group V (178 : 160), and was therefore assigned the attractiveness value of 100, with navy blue serge, in proportion, at 87. The results of all 32 cloths in the four groups were then combined in the light of the results from the fifth group, to give attractiveness ratings for the entire series. The calculation was done in two stages. As an example of the method of calculation, the leading pair selected from Group I (dark red (I) and purple) had an average landing ratio of 103·5 $\left(\frac{146 + 61}{2}\right)$ in Group V as compared with the ratio of 178 for black drill, or 58 with the latter at 100. Their relative attractiveness in Groups I and V of Table IV, reduced to 100, were 64 : 36 and 70 : 30, respectively, thus averaging 67 : 33. Dark red (I) was therefore set at 78 (67 per cent. of 2 × 58), and purple at 38 (33 per cent. of 2 × 58). The leading pairs selected from Groups II and IV were dark blue (II) and dark red (II), tropical suiting and black-filled nylon, respectively. These gave average landing ratios in Group V, as compared with black drill at 100, of 38·5 and 27·25, respectively, and, taking their relative attractiveness within the pairs into account, they were set at 40 (52 per cent. of 2 × 38·5), 37 (48 per cent. of 2 × 38·5), 31 (57 per cent. of 2 × 27·25) and 23·5 (43 per cent. of 2 × 27·25). In the second stage the attractiveness rating of the remaining six cloths in each of the four groups was then determined as follows:—in the Group I series, the best pair, dark red and purple, between them amassed a landing rate of 89 (57 + 32) in Group I and have been together rated at 116 (78 + 38) in relation to black drill at 100. The landing rates of the other cloths in Group I were therefore multiplied by $\frac{116}{89}$, giving 46 for dark blue and corresponding figures for the other colours. Similarly, the landing rates in Groups II, III and IV were multiplied by $\frac{77}{62}$, $\frac{187}{116}$ and $\frac{54}{156}$, respectively.

The attractiveness ratings for cloths both on army personnel and on robots are listed in Table V. It may be seen that the two sets of ratings are in fairly good agreement. The final attractiveness rating is taken as the average of the two figures for each cloth.

TABLE V.

Attractiveness ratings of 32 cloths based upon landing-rates of *Aëdes* mosquitos (in rotation experiments).

No.	Group	Type of cloth	Personnel	Robots	Average
A-1	III	Cloth, cotton drill, satin (work clothing) black	100	100	100
A-2	III	Cloth, worsted serge, 9 oz. (navy blue) ..	100	87	94
E-1	I	Dark red Munsell 2.5 R 3/8	96	78	87
E-4	I	Purple Munsell 2.5 P 3/8	82	38	60
A-9	III	Cloth, worsted serge, 9 oz. (AF blue) ..	63	49	56
E-5	I	Light red Munsell 2.5 R 7/8	65	42	54
A-10	III	Cloth, drill, VD 59 (# 1 drill) black, not mercerised	62	44	53
B-1	II	Black crêpe	35	71	53
A-11	III	Cloth, nylon canvas (S298) blue	61	29	45
A-12	IV	Cloth, rayon/wool (tropical dress)	57	31	44
A-13	III	Cloth, nylon/rayon, blue (U.S. raincoat) ..	56	32	44
E-3	I	Dark blue Munsell 2.5 B 3/8	40	46	43
A-14	III	Cloth, drill VD 59 (# 1 drill) black, mercerised	53	32	42
B-3	II	Dark blue satin # 2181	46	40	43
E-8	I	Light blue Munsell 2.5 B 4/8	42	42	42
B-8	II	Luminescent flag red	40	43	42
B-7	II	Dark red satin # 3774	44	37	40
A-18	IV	Cloth, flannel shirting (khaki)	39	40	40
B-5	II	Dark green satin # 198	30	41	36
A-15	IV	Cloth, nylon canvas (with 20% Viscose containing carbon black)	47	23	35
B-11	II	White satin # 100	21	43	32
A-16	III	Cloth, cotton drill, satin (work clothing) white ..	43	15	29
A-5	IV	Cloth, tentage VP15 (OD)	33	25	29
A-4	IV	Cloth, cotton drill (perfection drill for bush clothing)	38	17	28
E-6	I	Yellow Munsell 2.5 Y 7/8	30	13	22
A-6	IV	Cloth, nylon canvas (S298) brown	23	18	20
B-6	II	Luminescent Kelly green	12	26	19
E-7	I	Light green Munsell 10.0 GY 7/8	26	8	17
E-2	I	Dark green Munsell 10.0 GY 3/8	22	9	16
A-7	IV	Cloth, nylon canvas (S298) green	15	7	11
A-3	IV	Cloth, nylon canvas (S298) OD 7 olive ..	12	5	8
B-9	II	Luminescent arc yellow	3	11	7

The two most attractive cloths were given the rating of 100.

The reflectivities of the cloths, as measured by their percentage reflectance values at a series of wave-lengths of visible and ultra-violet light, are listed in Table VI in parallel order to that in Table V. It will be seen that there is a tendency for the cloths with the least reflectivity to be the most attractive for mosquitos, while the majority of the least attractive cloths are those with high reflectivities. However, the correlation is not regular, a fact which might be attributed to the great variety of material and texture of the cloths tested.

Therefore, comparisons were made within the series of eight flannels in Group I, the seven satins in Group II, and the five nylon canvases, three cotton drills and two worsted serges in Groups III and IV. The total brightness of each of the cloths in question was calculated by summing the reflectance values for the various wave-lengths, correcting and weighting each reflectance value by the energy value of diffuse daylight at that wave-length. The energy distribution of the solar spectrum, from which diffuse daylight does not significantly differ, follows the emissivity of a black body according to Planck's energy distribution law, from which the energy distribution figures were taken (Jahnke & Emde, 1945). The attractiveness values obtained for the cloths both in the paired and the rotating experiments are compared in Table VII with the total brightness value, in arbitrary units, both in the broad range between 300 and 700 mμ (including all visible and ultra-violet light) and in the narrow range between 475 and 625 mμ (including orange, yellow, green and green-blue light).

TABLE VI.

Percentage reflectances of cloths in visible and ultra-violet light.

Cloth No.	Wave-length in millimicrons								
	300	350	400	450	500	550	600	650	700
A-1 ..	1	2	2	2	2	2	2	2	2
A-2 ..	2	2	2	2	2	2	1	2	5
E-1 ..	3	4	5	4	2	2	13	17	40
E-4 ..	3	6	21	16	6	4	6	6	21
A-9 ..	2	4	5	6	5	4	4	4	10
E-5 ..	3	16	28	33	24	26	58	62	64
A-10 ..	2	2	2	2	2	2	2	2	2
B-1 ..	1	1	1	2	2	2	2	2	2
A-11 ..	3	5	6	6	4	3	3	3	4
A-12 ..	4	7	7	7	8	10	10	11	16
A-13 ..	3	5	5	5	4	3	3	3	8
E-3 ..	3	5	4	12	19	4	1	1	4
A-14 ..	2	2	2	2	2	2	2	2	2
B-3 ..	2	10	1	5	5	3	2	3	12
E-8 ..	2	8	8	22	30	11	3	2	18
B-8 ..	64	10	14	25	23	22	42	85	88
B-7 ..	6	21	18	5	3	5	19	64	77
A-18 ..	3	5	6	7	9	11	13	15	19
B-5 ..	2	7	3	4	17	11	4	3	4
A-15 ..	3	7	5	4	5	5	6	5	5
B-11 ..	33	60	68	76	84	86	88	89	89
A-16 ..	49	64	80	84	88	85	84	86	89
A-5 ..	2	5	5	6	6	9	9	8	9
A-4 ..	3	4	8	7	9	12	12	14	17
E-6 ..	3	8	8	9	11	45	49	48	62
A-6 ..	5	4	4	4	5	6	5	5	36
B-6 ..	7	14	8	9	34	17	7	5	7
E-7 ..	3	9	11	13	42	44	26	13	15
E-2 ..	4	2	2	1	9	8	2	1	1
A-7 ..	4	5	5	6	12	10	9	9	19
A-3 ..	4	5	4	5	11	8	9	9	24
B-9 ..	10	20	23	26	51	56	83	86	87

It will be seen that there is a definite tendency for the attractiveness to vary inversely with the brightness of the cloth. Therefore the figures for the flannels, satins and nylons were subjected to statistical analysis to determine the correlation coefficients (r).* The values of r obtained are shown in Table VIII. It is

---

* Where $r = \frac{\Sigma dxdy}{\sqrt{\Sigma(dx)^2 + \Sigma(dy)^2}}$, dx being the deviation of each value from the average of the attractiveness ratings x, and dy being the deviation of each value from the average of the brightness values y (Snedecor, 1946, p. 138).

TABLE VII.

Comparison between attractiveness ratings of cloths and their brightness as measured by reflectivity of energy of solar spectrum.

		Attractiveness		Brightness	
		Paired (actual counts)	Rotating (counts reduced to max. 100)	300–700 mμ	475–625 mμ
Munsell flannels :					
E-1	Dark red	593	87	1517	329
E-5	Light red	388	54	5761	2139
E-4	Purple	363	60	1634	422
E-3	Dark blue	404	43	1026	501
E-8	Light blue	331	42	1973	914
E-6	Yellow	203	22	4369	2082
E-2	Dark green	319	16	561	391
E-7	Light green	199	17	3405	2276
Satins :					
B-7	Dark red	456	40	3712	526
B-8	Lumin. red	350	42	5606	1731
B-3	Dark blue	404	42	857	225
B-5	Dark green	372	36	1053	658
B-6	Lumin. green	316	19	2044	1196
B-11	White	316	32	12344	5191
B-9	Lumin. yellow	57	7	8031	3733
Nylon Canvases :					
A-11	Blue	—	45	675	202
A-15	Black-filled	—	35	815	321
A-6	Brown	—	20	1244	322
A-7	Green	—	11	1433	628
A-3	Olive-drab	—	8	1407	555
Cotton Drills					
A-1	Black	—	100	311	121
A-16	White	—	29	13047	5190
A-4	Olive (Perfection)	—	28	1573	661
Worsted serges :					
A-2	Navy blue	—	94	351	102
A-9	Air Force blue	—	56	801	263

TABLE VIII.

Correlation coefficients (r) between total reflectivity and attractiveness of cloths to female *Aëdes* mosquitos.

Cloth	Range of wave-length	
	300–700 mμ	475–625 mμ
Flannels (8 cloths)		
Paired tests (Table I)	—0·35	—0·68
Rotating tests (Table V)	—0·23	—0·44
Satins (7 cloths)		
Paired tests (Table II)	—0·47	—0·62
Rotating tests (Table V) . .	—0·30	—0·49
Nylon Canvases (5 cloths)		
Rotating tests (Table V)	—0·97	—0·88

seen that the correlation coefficients are all negative, indicating that the relationship is an inverse one. The correlation for the series of nylon canvases is especially close; the values of −0·97 and −0·88 indicate, for the three degrees of freedom involved, a complete correlation at the 1 per cent. and 5 per cent. levels of significance, respectively. This high degree of correlation rarely occurs in biological data. The correlation coefficients obtained with the flannels and satins, which were between −0·44 and −0·68 for reflectivity in the narrow range, were more typical of the degree of biological correlations. It is apparent from Table VIII that the correlation of attractiveness with reflectivity is much closer in the narrower range between blue and orange light (475–625 mμ) than in the broad range of all visible and ultra-violet light (300–700 mμ).

TABLE IX.

Correlation coefficients (r) between percentage reflectivity (for ultra-violet and visible light) and attractiveness of cloths to *Aëdes* mosquitos.

Cloth	Wave-length at which percentage reflectivity is considered :—								
	300 mμ	350 mμ	400 mμ	450 mμ	500 mμ	550 mμ	600 mμ	650 mμ	700 mμ
Flannels									
Paired tests ..	−·03	−·22	−·04	−·11	−·37	−·76	−·29	−·12	+·04
Rotating tests ..	−·28	−·02	−·14	+·09	−·48	−·56	−·10	+·05	+·18
Satins									
Paired tests ..	−·22	−·11	−·20	−·29	−·52	−·58	−·67	−·57	+·18
Rotating tests ..	−·19	−·11	−·05	−·14	−·40	−·45	−·45	−·16	−·10
Nylon canvases									
Rotating tests ..	−·81	+·37	+·78	+·02	−·93	−·96	−·88	−·92	−·72

The attractiveness ratings for the three types of fabric were then correlated with individual percentage reflectance values for selected wave-lengths at 50–mμ intervals (Table IX). It will be seen that the correlation coefficients are closest to −1 when the reflectivity at the 500, 550 and 600 mμ wave-lengths is considered. There is no correlation at wave-lengths below 450 mμ, from the violet into the ultra-violet, down to a wave-length of 300 mμ. The correlation coefficients drop sharply at 650 mμ (red) and there is no correlation at all at a wave-length of 700 mμ.

Reflectances in the infra-red range had been determined for 16 of the cloths tested. When these values were compared with the attractiveness ratings it was evident that no correlation existed, negative or otherwise. Statistical analysis of the figures for five cloths of different colour but of identical texture showed definitely that no correlation existed between attractiveness and infra-red reflectance.

Discussion of Results.

The results summarised in Tables V to IX show that in general the attractiveness of a cloth as a landing surface for adult female *Aëdes* mosquitos is an inverse function of its brightness as measured by its reflectivity for light between 475 and 625 mμ in wave-length. The correlation coefficient of attractiveness with brightness in this range is roughly the average of the three correlation coefficients obtained for the individual wave-lengths of 500, 550 and 600 mμ, respectively (*cf.* Table VIII, col. 3, with Table IX, cols. 6–8). This in itself is evidence for the view of Gjullin that colours are chosen by mosquitos on the basis of their spectral reflectances and not by the ability to distinguish colours.

In the present work a number of factors has interfered with this correlation, of which the most important is the texture of the clothing. For example, although the average attractiveness rating of the nylons tested was only 24, that of the satins was 31, the flannels 43, the cotton drills 52, and the worsted serges 75. Naturally these figures have no quantitative meaning since the colours varied between the various types of cloth, but the qualitative differences are nevertheless present.

Another factor is the floristic setting in which the experiments were conducted. This was a spruce forest with a ground cover of moss and ericaceous plants, giving a sombre olive-green effect varied with darker and lighter hues. In these experiments the green cloths were less attractive than their low reflectivity would seem to warrant. This is especially marked in the case of the dark green flannel, which had one of the lowest reflectivities but was one of the least attractive cloths. Dark green satin, light green flannel and luminescent green satin were all less attractive than their low reflectivity in the lower visible range would indicate. In the nylons, the green and olive-drab colours did have the highest reflectivities, and this was the main reason why the negative correlation coefficients were high with nylons; and the aberrant performance of the green colours in the flannels and satins was an important factor lowering the correlation coefficients for these fabric groups.

On the other hand the bright red cloths, possibly owing to their conspicuousness in the green setting, were quite highly attractive. The attractiveness of simultaneous contrast is already well known in the case of visual responses of insects. The attractiveness ratings of light red flannel and luminescent red satin were considerable despite quite a high reflectivity throughout the entire range of visible light. The dark red flannel was almost the most attractive cloth, being surpassed only by black drill and navy blue serge.

The blue colours gave results agreeing well with the negative correlation of attractiveness and brightness. A good example of this is furnished by the two worsted serges, where navy blue was twice as attractive as air force blue while having half its reflectivity (see Table VII). In general, the blue cloths were less attractive than the red, and more attractive than the green.

Yellow flannel was one of the least attractive fabrics, and luminescent yellow satin was the least attractive of all the cloths. The white cloths with the highest reflectivities of all were not the least attractive of the fabrics tested. White satin was more attractive than luminescent yellow and luminescent green, while white drill was more attractive than the olive-drab Perfection drill. It is possible that the dark cast imparted to white by the underlying clothing (khaki shirt for army personnel, grey felt undershirt for robots), coupled with the conspicuous contrast with the setting of spruce foliage, enhanced its attractiveness.

As expected, black cotton drill was the most attractive cloth. For an explanation of the inferior attractiveness of the two VD-59 drill (A-10 and A-14 in Table V) and the black crêpe, it would be necessary to investigate texture or olfactory characteristics, because their reflectivities are no greater than that of the black drill. The order of attractiveness of colours found in this investigation may be compared with that found by other workers with *Aëdes* mosquitos as follows:—

A. aegypti: black, red, brown, white, blue, green, yellow (Brett, 1938).*
A. lateralis Mg.: black, blue, red, brown, green, yellow, white (Gjullin, 1947).

---

* This order was obtained when the colours were tested against black; when tested against white, the order was red, black, brown, green, blue, yellow, white.

A. dorsalis (Mg.): black, blue, red, green, brown, yellow, white (Gjullin, 1947).

A. hexodontus Dyar and associated species: black, red, brown, blue, green, yellow, white (Gjullin, 1947).

A. punctor and associated species: black, red, blue, brown, green, white, yellow (present investigation).

Naturally, these ratings will vary according to the brightness of the samples selected to represent the colour. It should be pointed out here that the dark blue used in Group I was only a shade darker than the light blue.

A feature of this investigation is the lack of correlation of attractiveness with reflectivity in the ultra-violet range between 450 and 300 mμ. This is surprising in view of the fact that many insects, as exemplified by the honey bee and the house-fly, can see far into the ultra-violet (Wigglesworth, 1950), and that many insects exhibit a peak of responsiveness to low light intensities at a wave-length of 365 mμ in the ultra-violet (Weiss, 1946). The finding with *Simulium venustum* Say (Davies, 1951), that the dark cloths with the highest ultra-violet reflectances were the most attractive, was not duplicated in these experiments with *Aëdes*; for example with the flannel clothing, both dark red (the most attractive) and dark green (almost the least attractive) reflectivities were low, while in the ultra-violet and violet range, in purple and dark blue, they were high.

The lack of correlation between attractiveness and reflectivity in the infra-red range is not surprising. For example, it has already been shown that infra-red radiation is not a factor in the response of *Aëdes aegypti* to a warm body (Peterson & Brown, 1951). This lack of correlation with attractiveness extends down into the red end of the spectrum, possibly as far as a wave-length of 650 mμ (see Table IX). The red cloths are highly attractive despite being highly reflective for red light down to a wave-length of 600 mμ, and the same applied in less degree to purple.

Summary.

A series of 32 cloths, including 8 flannels dyed to Munsell standard colours, seven coloured satins and 17 service fabrics, were tested for their attractiveness to northern Canadian *Aëdes* mosquitos, and were assessed for their reflectivity of visible and ultra-violet light.

Their attractiveness was found to vary inversely with their reflectivity or brightness, although the different textures represented in the series tended to obscure the generalised relationship.

When comparisons were made within a series of identical texture, the correlation was good in the range between 475 and 625 mμ wave-length, but was not present in the red or infra-red, nor in the violet and ultra-violet ranges of wave-length.

Green tended to be less attractive, and white more attractive, than was expected from this relationship. For colour values of similar lightness or darkness, the order of attractiveness to *Aëdes punctor* and associated species was black, red, blue, brown, green, white, yellow.

Acknowledgements.

This investigation was made possible by the Defence Research Board of Canada, which supported it financially as Project No. D49-68-20-07. The author records his indebtedness to Mr. A. C. Jones of its Environmental Protection Section, who procured the materials and arranged their optical assessment. The reflectance values were determined by Mr. W. E. K. Middleton of the National Research Council of Canada, to whom thanks are due for his willing help and ideas. The service cloths were supplied by Col. H. A. Delcellier, Directorate of Inter-Service Development, Canadian Army. The Munsell flannels were supplied by the Ontario Research Foundation, through the kindness of Dr. D. M. Davies, whose helpful interest has meant much to this investigation.

The project was financially supported by the Defence Research Board and the Department of Agriculture, Canada, through Dr. C. R. Twinn, Head, Veterinary and Medical Entomology Unit, Division of Entomology, to whom the author offers his sincere thanks. Valuable assistance in the experiments was given by Mr. D. L. Watson and Mr. L. M. Fisher, Division of Entomology, and also by Major Felix Ingham, R.A.M.C.

References.

Brett, G. A. (1938). On the relative attractiveness to *Aëdes aegypti* of certain coloured cloths.—Trans. R. Soc. trop. Med. Hyg., **32**, pp. 113–124.

40 39 Brown, A. W. A. (1951). Studies of the responses of the female *Aëdes* mosquito. Part IV. Field experiments on Canadian species.—Bull. ent. Res., **42**, pp. 575–582.

Davies, D. M. (1951). Some observations of the number of black flies (Diptera, Simuliidae) landing on colored cloths.—Canad. J. Zool., **29**, pp. 65–70.

[illegible] Gjullin, C. M. (1947). Effect on clothing color on the rate of attack of *Aëdes* mosquitoes.—J. econ. Ent., **40**, pp. 326–327.

Jahnke, E. & Emde, F. (1945). Tables of functions, with formulae and curves. 4th edn. Appendix pp. 44–47.—New York, Dover Publ.

Nickerson, D. (1948). Color and its description.—Bull. Amer. ceram. Soc., **27**, pp. 47–55.

40 [illegible] Peterson, D. G. & Brown, A. W. A. (1951). Studies of the responses of the female *Aëdes* mosquito. Part III. The response of *Aëdes aegypti* (L.) to a warm body and its radiation.—Bull. ent. Res., **42**, pp. 535–541.

Snedecor, G. W. (1946). Statistical methods. 4th edn.—Ames, Iowa St. Coll. Pr.

Taylor, A. H. (1920). The measurement of diffuse reflection factors and a new absolute reflectometer.—J. opt. Soc. Amer., **4**, pp. 9–23.

Weiss, H. B. (1946). Insects and the spectrum.—J. N. Y. ent. Soc., **54**, pp. 17–30.

Wigglesworth, V. B. (1950). The principles of insect physiology. 4th edn., pp. 142–147. London, Methuen.

41 [illegible]

AIRCRAFT APPLICATIONS OF INSECTICIDES IN EAST AFRICA.

V.—THE DEPOSITION IN OPEN COUNTRY OF A COARSE AEROSOL RELEASED FROM AN AIRCRAFT.

By D. Yeo and B. W. Thompson.
Colonial Insecticide Research Unit, Arusha, Tanganyika.

Y.L.

The term " aerosol " is used loosely to describe insecticidal clouds consisting of droplets whose diameters vary from a few microns to approximately 200 microns. In this paper it will be assumed that a " coarse aerosol " is one in which the drop spectrum covers approximately this range, but which in addition has a mass median diameter of the order of 80 microns. Such droplets are often used in an *ad hoc* fashion to control insect pests, but there is little systematic knowledge of the effect upon their behaviour of changes in meteorological and other field conditions. Aerosol behaviour is complex. It depends upon the degree of atmospheric turbulence, the type and density of the vegetation cover, the drop spectrum, and the method of application of the aerosol.

When an aerosol is released over woodland there are two distinct meteorological problems that concern its eventual distribution among the trees. The first is the effect of the atmospheric turbulence within the free air above the canopy; the second is the nature of the air movement within the canopy, which is a function of the nature and density of the trees and the condition of the free air (see, for instance, Geiger, 1950). It is evident therefore that within the space through which the aerosol falls the degree of atmospheric turbulence varies with height in an extremely complex fashion. Furthermore, the efficiency with which droplets impact upon obstacles is dependent, among other factors, upon the droplet size and the wind speed (see, for example, Langmuir & Blodgett, 1949). The behaviour of aerosols under field conditions is, therefore, such an abstruse problem that simplification of the many variables is essential if ordered knowledge is to be obtained.

As a necessary preliminary basis to our work the behaviour of aerosols in open country was investigated. This paper describes the deposition upon a stretch of open country of a coarse aerosol released from a low-flying aircraft. The experiments form part of an investigation into the possibilities of using insecticides to control insect pests in East Africa, and have been mainly empirical. It has been assumed that a correlation does exist between deposition and meteorological conditions, and an attempt has been made to show this correlation in terms of relatively simple meteorological measurements.

The Effect of Meteorological Conditions.

The variation of temperature with height is of fundamental importance in determining the motion of air. When a parcel of air is forced to rise, it undergoes a fall in pressure since it immediately takes up the pressure of its environment; the parcel expands, and its density, relative to that of the surrounding air, is determined by its absolute temperature. An atmosphere in neutral equilibrium is one in which a parcel of air, if moved from one level to another, always has the density of the surrounding air; in this case the temperature decreases with height at a rate known as the adiabatic lapse rate, which in dry air is approximately 1·8°F. (1°C.) per 100 m. If the temperature decreases more rapidly than this, superadiabatic lapse rate conditions exist; the atmosphere is unstable, and convective motions will develop. If, on the other hand, the temperature decreases less rapidly with height, or increases with height, the atmosphere is stable, and upward motions tend to be inhibited; the most common condition of this case is the "inversion" where temperature increases with height.

When the structure of atmospheric movement is analysed in detail, it is found that air motion near the ground is characterised by rapidly fluctuating gusts, lulls, and changes in wind direction from the mean direction, and that these variations may occur even during inversions, although they are then generally very much less pronounced than during adiabatic or superadiabatic lapse conditions. With strong inversions and low wind speeds, air flow approaches a smooth or laminar state, such turbulence as exists resulting from irregularities in the ground surface which cause overturning of air by friction and the consequent development of an eddy motion; this effect naturally increases as the wind speed increases and an eventual result may be the destruction of the initial inversion. Under superadiabatic lapse rate conditions frictional eddying is enhanced by thermal convection and the degree of atmospheric turbulence is therefore high.

An hypothesis of Hesselberg and Björkal (1921), that the wind eddies in the atmosphere have a velocity distribution similar to that given by Maxwell for molecular velocities, was tested by Best (1935), who showed that the eddies along the mean wind direction have a distribution which can be represented by a suitable error function. Using his data, and some comparative results by Scrase (1930) of the relative magnitude of eddies in the horizontal and vertical directions, it is possible to express the total random movement of air in a vertical direction by the equation

$$M = \frac{0{\cdot}75u}{100\sqrt{\pi k}} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (1)$$

where M = total random movement in a vertical direction in unit time,
u = mean wind speed, and
k = a constant of the eddy distribution, of the order of 10^{-3}.

Thus M may be calculated for various values of u and k. It is found to be comparable to distances fallen under gravity by droplets less than 100 microns in diameter, except in the case of very low wind speeds. It is reasonable to expect, therefore, that coarse aerosols will be considerably affected by the degree of atmospheric turbulence, and that it will not be possible to explain their behaviour in terms of the terminal velocities of the droplets and the mean wind speed, as is the case for droplets whose diameters are greater than 200 microns approximately (see, for instance, Gunn & others, 1948*a*, *b*).

Richardson (1920, 1925) deduced a dimensionless parameter which was intended to specify a critical point in the conditions of turbulence in the atmosphere. This parameter, now known as Richardson's Number, is given by the equation

$$Ri = \frac{g\left(\frac{\partial T}{\partial z} + \Gamma\right)}{T\left(\frac{\partial u}{\partial z}\right)^2} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (2)$$

where Ri = Richardson's Number,
g = acceleration due to gravity,
T = mean air temperature in °Abs.,
u = mean wind speed,
z = height above the ground, and
Γ = the numerical value of the dry adiabatic lapse rate.

Thus Ri is positive under atmospheric stability, zero with dry adiabatic lapse rates, and negative during superadiabatic lapse rate conditions. Richardson's Number is intended to specify the critical point at which atmospheric conditions change from those in which turbulent eddies tend to increase to those in which eddies tend to die out. Whilst the exact value of the parameter for this critical point, as deduced by Richardson and subsequent investigators, is open to doubt (Sutton, 1949), and although Calder (1949) has shown that Richardson's theoretical analysis contains certain limitations, Richardson's Number has become increasingly recognised in meteorology as a measure of the degree of atmospheric turbulence. It is, however, of chief value over a particular ground surface and becomes a doubtful value for comparative measurements over different surfaces since $\left(\frac{\partial u}{\partial z}\right)$ varies according to the nature of the ground surface (Deacon, 1949). Richardson's Number is therefore too delicate a parameter to relate to aerosol behaviour in the field of practical operations.

The experiments described here were carried out over a period of more than a year, and it was quite impossible to maintain constant the height of the grass cover over the experimental area. Such variations would be the usual case in practice, and it is therefore necessary to have a measure of atmospheric turbulence that is applicable to a wide range of surface types, even at the expense of accuracy from the theoretical viewpoint. An investigation by Deacon (unpublished) seems to give a parameter of practical value. This parameter is related to Richardson's Number, and since the meteorological work in this paper depends upon it, a modified account of its derivation is given in some detail.

Considering a narrow layer of air, Ri is of the form

$$\frac{g}{T}\left\{\frac{T_2 - T_1 + \Gamma.\delta h}{(u_2 - u_1)^2}\right\} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (3)$$

where T_1, T_2 and u_1, u_2 are respectively the temperatures and mean wind speeds at the bounding heights z_1 and z_2, and $\delta h = z_2 - z_1$. Assuming that g and T are constant, we have

$$Ri \propto \left\{\frac{T_2 - T_1 + \Gamma.\delta h}{(u_2 - u_1)^2}\right\}$$

Now assume that the ratio $R = \frac{u_2}{u_1}$ is also a function of Ri, i.e., that

$$R = \frac{u_2}{u_1} = f\left\{\frac{T_2 - T_1 + \Gamma.\delta h}{(u_2 - u_1)^2}\right\}$$

where f denotes functional dependence. Then

$$R = f\left\{\frac{T_2 - T_1 + \Gamma.\delta h}{u_1^2\,(1 - R)^2}\right\} = f\left\{\left(\frac{T_2 - T_1 + \Gamma.\delta h}{u_2^2}\right)\left(\frac{R}{R-1}\right)^2\right\}$$

Solving these equations explicitly for R, we have

$$R = f_1\left\{\frac{T_2 - T_1 + \Gamma.\delta h}{u_1^2}\right\} = f_2\left\{\frac{T_2 - T_1 + \Gamma.\delta h}{u_2^2}\right\} \quad \ldots \quad \ldots \quad (4)$$

Deacon showed that over a particular surface R was uniquely related to F, where F is given by the equation

$$F = \left\{\frac{T_2 - T_1 + \Gamma.\delta h}{u^2}\right\} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (5)$$

He uses the values

T_2 = absolute temperature at a height of 17·1 m.,
T_1 = absolute temperature at a height of 1·2 m.,
u = mean wind speed at 2 m., and
R = the ratio $\frac{\text{mean wind speed at 2 m.}}{\text{mean wind speed at 1·2 m.}}$

Since equations (4) follow from the assumption that Ri and R are uniquely related, it follows that Ri is a unique function of F, within the limits of Deacon's observations. It is likely that the relationship does not apply when large temperature gradients exist.

The advantage of F lies in the fact that u is probably less sensitive to changes in the nature of the surface than is $\left(\frac{\partial u}{\partial z}\right)$, provided that the wind measurement is not made too close to the ground. It would therefore be expected that F would show less change than Ri with surface roughness, and could be used as a measure of atmospheric turbulence over a considerable range of surface types. The numerical value of F obviously depends upon the layer of air for which it is calculated. For our work the following values were used:—

T_2 = air temperature (in °F.) at 10 m.
T_1 = air temperature (in °F.) at 2·5 m.
u = mean wind speed (in f.p.s.) at 5 m.

The Meteorological Observations.

A light, open, wooden tower, designed to cause as little obstruction as possible to the airflow, was erected on the aerodrome at Arusha, Tanganyika. This was the focal point of the earlier experiments, although some of the later results were obtained on an open, grassy plain about 20 miles from Arusha. The observation tower was 10 m. high, the height being chosen partly because it was the maximum height for which a sturdy erection could be made from the materials immediately to hand, and partly because it was near the lower limit of heights from the ground, or vegetation cover, likely to be flown by aircraft.

The mean wind speeds were measured at heights of 2·5, 5 and 10 m. Sheppard three-cup anemometers were used, since these are designed to give a high accuracy for this type of work. At the beginning and end of each trial, the average time of which was 8–10 minutes, the anemometers were started and stopped simultaneously, thus measuring the mean wind speeds over this period. It is worth recording that the wind profile proved to be nearly logarithmic in all but strong inversional conditions, so that the wind speed at 5 m. was usually equal to the arithmetic mean of the wind speeds at the other two heights. Only the wind speed at 5 m. was used in the calculation of F; the readings at the other heights were taken mainly for their purely meteorological value, although they did act as a valuable check upon the readings at 5 m.

Temperature observations were made at heights of 2·5, 5 and 10 m., using clockwork-driven Assmann psychrometers. Although not ideal for the measurement of temperature lapse rates, for which delicate recording equipment is highly desirable, they have the advantages of robustness and great portability, and can be used by relatively unskilled staff. They were mounted in light screens specially constructed to shield the psychrometers from radiation, and were read to the nearest 0·1°F. Owing to the continuous fluctuation of temperature during high superadiabatic lapse rate conditions, it was necessary to aspirate the psychrometers continuously and to read them as frequently as possible, in order to obtain good mean values of the temperatures at the different levels during the period of a trial. During inversions, of course, temperature fluctuations were small, and observations were easier to make and were more reliable.

Wind direction was carefully observed before each trial in order to determine the direction of the assessment layout and the aircraft track. A close watch was kept for changes in wind direction during the course of a trial, which was, perforce, abandoned if variations became marked. Such variations were usually most marked during conditions of strong inversions, and consequently many trials during periods of low turbulence were spoiled. This, allied to the fact that fewer occasions of low turbulence occurred than were expected, resulted in less observations of ground deposition under these conditions than would normally have been desirable. From a practical point of view, however, it is noteworthy that the extremely variable wind direction might cause uneven dosages even though the quieter atmospheric conditions are most suitable for high sedimentation of the aerosol.

Field and Assessment Methods.

For sprays consisting of droplets greater than 200 microns it is customary to use an extensive sampling system to measure the ground deposit. The aircraft is flown at right angles to the mean wind direction, along which several rows of sampling points are placed. The distances between the samples are chosen so that no undue importance is attached to any one sample. Such an arrangement involves the estimation of deposits at several hundred points. With aerosols, for which the assessment of deposits is more laborious in any case, so many samples would have seriously limited the number of trials that could have been done. Earlier (unpublished) work had suggested that a single row of sampling points gave a sufficiently accurate measure of the ground deposit under most conditions, and some accuracy was sacrificed by estimating deposits upon one such row. The sampling row was laid out along the mean wind direction; the aircraft was flown at right angles to it. From the emission rate of solution from the aircraft, and the ground speed of the aircraft, the amount of solution emitted per unit distance of aircraft track could be calculated. Aircraft heights were measured with a clinometer.

Although it was necessary to measure the average meteorological conditions over a period of several minutes, the emission of the aerosol that deposited upon the sampling points took place in an immeasurably short period. Average meteorological conditions were therefore only a crude measure of the turbulent eddies affecting the aerosol behaviour, except possibly during periods of very low turbulence. To overcome this to some extent, four emission runs were made during a period of 8–10 minutes. This reduced the probability of assessing a ground deposit which had been formed during a period when the actual meteorological conditions differed widely from average conditions. It also increased the ground deposit, and thus assisted its estimation.

The ground deposit was estimated in two ways. A small quantity of the oil-soluble dye, Waxoline Red, was added to the solution; the ground deposits were collected upon absorbent paper, extracted with petroleum ether in a Soxhlet, and estimated using a Spekker absorptiometer. In this way equivalent dosages of DDT, or of volumes of original solution, were estimated. In addition, glass plates, coated with magnesium oxide, were used to measure the actual volumes of the ground deposits, and to obtain data upon the drop spectra. To obtain subsidiary data upon the drop spectrum produced by the aircraft installation, cascade impactors (May, 1945) were also used. The colorimetric assessments gave a measure of the amounts of involatile material that were deposited, whereas size counts upon the oxide-coated plates estimated the actual volume of solution depositing upon the ground; some idea of evaporation effects was therefore obtained.

The Production of the Aerosol.

It was obviously wise to limit the number of variables and so only one drop spectrum was used in these experiments. The solution was a 10 per cent. w/v solution of technical DDT (80 per cent. p,p′isomer) in a solvent consisting of 1 part of Shell Power Kerosene to 1 part of Shell Diesoline. To this solution 0·75 per cent. w/v of Waxoline Red dye was added.

The aerosol was produced by a boom and nozzle system fitted to an Avro Anson aircraft. By means of a small windmill-driven pump the solution was forced, by a pressure of 150 lb. per sq. in., through 24 Bray 1 nozzles which were equally spaced along a boom underslung from the wings of the aircraft. The nozzles pointed forward into the slipstream. The emission rate was kept as constant as possible; some variation occurred due to blockages of some nozzles. The airspeed of the aircraft was approximately 110 m.p.h.

It will be shown later that it is difficult to determine precisely the drop spectrum of a coarse aerosol released from an aircraft, and further papers will show that the spectrum of the ground deposit, which is not the same as that of the aerosol produced by the aircraft installation, varies with the degree of atmospheric turbulence and the extent of the assessment downwind from the line of emission. To indicate the general form of the distribution of the droplet sizes in the ground deposit, however, the drop spectrum for a particular experiment when the value of *F* was + 40 × 10^{-3}, the mean wind speed at 5 m. was 3·1 f.p.s., and the assessment extended for 400 yards downwind from the line of emission is shown in fig. 1.

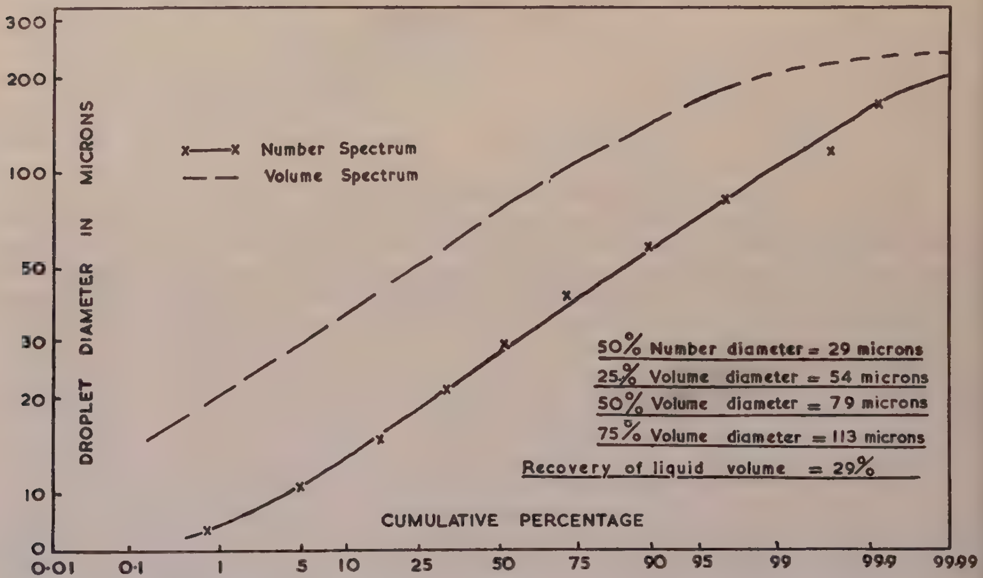


Fig. 1.—The drop spectrum of the ground deposit of a particular trial. The value of *F*, the measure of the degree of atmospheric turbulence, was + 40 × 10^{-3}, the mean wind speed at 5 m. was 3·1 f.p.s., and the recovery of liquid volume upon the area covered by the assessment was 29 per cent.

The Form of the Ground Deposit and its Variation with the Degree of Atmospheric Turbulence.

Two examples are given (fig. 2) of the variation in ground dosage with distance downwind from the line of emission. Actual values are recorded, and no corrections have been applied for variations in emission rates, aircraft heights, or for deviations in wind direction from the predicted direction that was used when laying out the assessment points. For convenience the data have been plotted upon log-log paper; apart from near the emission line the relationship between log dosage and log distance is roughly linear, indicating that the dosage falls off at a rate that is approximately a power function of the distance.

It is evident from the graphs that random variations in dosage are very considerable.

It was decided that a rational way to analyse the data would be to record the deposits in terms of the amount of DDT that was emitted from the aircraft, and to sum the deposits up to various values of the time interval elapsing after production of the aerosol. The aerosol cloud is spread out both vertically and laterally by turbulence, and the deposit at any point is laid down over a period of at least several seconds: except near the aircraft, however, a good measure of the average time interval between production of the droplets and their deposition at a sampling point is given by the ratio

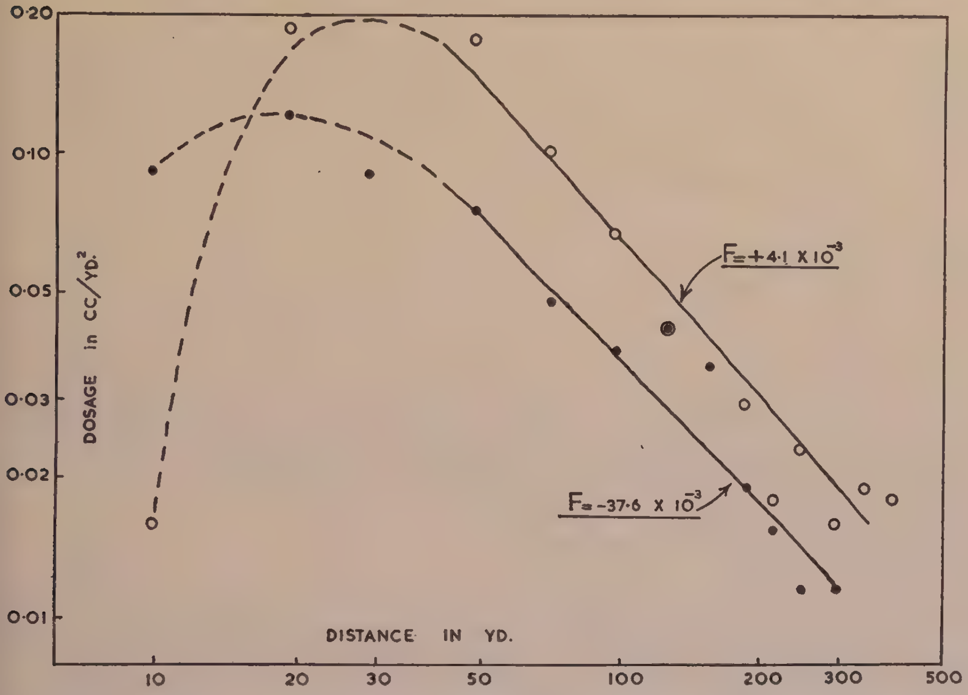


Fig. 2.—Two typical distributions of the ground deposit. On log-log paper the ground dosage is plotted against distance. Actual values are recorded, with no corrections for variations in emission rates, aircraft heights, or for deviations in wind directions from the predicted direction used in laying out the assessment points.

$$t = \frac{\text{distance downwind of the sampling point}}{(\text{mean wind speed at 5 m.})}$$

If the wind direction differed from the predicted wind direction by an angle θ, then time intervals were calculated by multiplying the ratio given above by the factor $1/\cos\theta$. Small variations in aircraft height occurred and corrections were made for these by multiplying the ground dosages by a factor

$$\frac{\text{aircraft height in ft.}}{30}$$

and it is these corrected values that have been analysed in detail. The application of this correction factor for height variations is probably reasonable when variations are small, but it cannot be applied when errors are large.

In fig. 3 the proportion of DDT that is deposited within a time interval of 90 seconds is plotted against *F*, the measure of the degree of atmospheric turbulence. The value of the proportion for $F = +80{\cdot}5 \times 10^{-3}$ is doubtful because the aircraft height was considerably different from 30 ft. The limits of the important meteorological measurements were as follows:—

the temperature difference $T_{10} - T_{2\cdot5}$: − 2·5°F. to + 3·6°F.
the mean wind speed at 5 m.: 3·1 f.p.s. to 20·3 f.p.s.

The correlation coefficient between *F* and the amount deposited within 90 seconds is 0·91 for the thirty observations plotted in fig. 3, so it is evident that, although the scatter of the points is large, a high correlation exists and the deposit is greatest during strong inversions and low wind speeds.

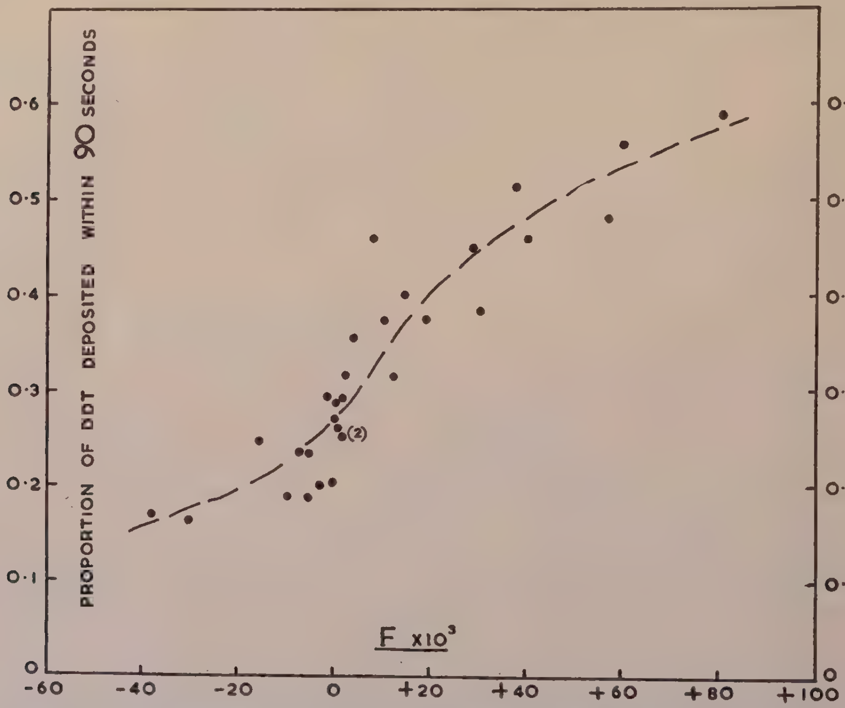


Fig. 3.—The proportion of DDT that is deposited within a time interval of 90 seconds after emission of the aerosol, plotted against *F*, the measure of the degree of atmospheric turbulence. The aircraft height was 30 ft.

The data were then grouped according to their values of *F*, and the variation with time of the proportion deposited was calculated for each convenient group. The results are given in fig. 4, where the proportion, on a linear scale, is plotted against time interval on a logarithmic scale. These graphs show that, for high positive values of *F*, deposits are greatest for all time intervals considered and that the total deposit increases most rapidly with time interval. For intervals greater than 15 seconds, the graphs are also very nearly linear, which indicates that, apart from the initial deposits, the rate of deposition is inversely proportional to the time interval.

This approximate linearity between the proportion deposited and log time interval is probably coincidental, and may not apply to greater time intervals. If the drop spectrum had consisted of large droplets, the deposition would have been complete within a short time, and the graphs of fig. 4 would have been concave to the time axis and would have levelled off at a value of unity for the proportion. A more fundamental analysis would be the study of the deposition of droplets of various sizes; this is being done, but the analysis is long and laborious and the results will be presented in a later paper. A preliminary study shows that the deposition of the smaller droplets is most affected by atmospheric turbulence, as would be expected.

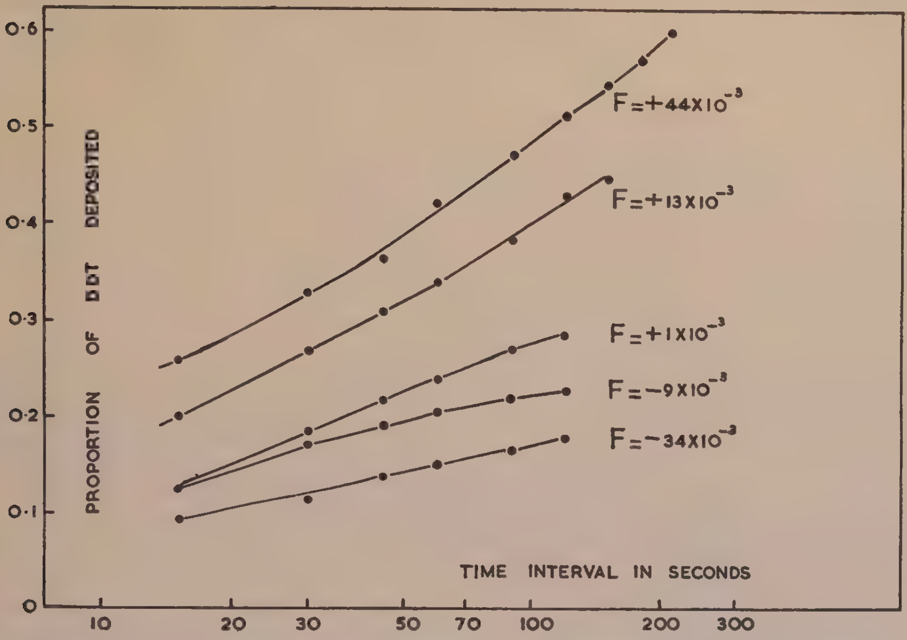


Fig. 4.—The variation with time interval of the proportion of DDT deposited upon the ground. The data have been grouped conveniently according to their values of *F*.

The drop spectrum given in fig. 1 was determined under conditions of relative calm, and it may be seen that only 2 per cent. of the droplets in the ground deposit had diameters less than 10 microns. Samples taken with cascade impactors placed near the line of emission, however, showed that in fact some 80 per cent. of the droplets produced by the aircraft installation were in this small size range, although they contained less than 5 per cent. of the DDT (for similar results see Hocking & Yeo, 1953). It is evident, therefore, that such small droplets are not deposited appreciably within any useful time interval after production of the aerosol, and it would be uneconomical to attempt to use them to produce a deposit upon the ground surface or upon low vegetation. It is also evident that the spectrum of the ground deposit gives only a partial measure of the drop spectrum of the aerosol; this is also true of the samples taken with the cascade impactor, since these instruments do not sample accurately droplets greater than 50 microns in diameter, so the exact drop spectrum of the aerosol is not known.

The variations shown in figs. 3 and 4 may be used to show how the ground deposit varies with the time of day, if adequate meteorological measurements are made. Climatological surveys of turbulence are being carried out in East Africa, and these will be related to aerosol behaviour in subsequent papers, but it is highly likely that in most tropical areas coarse aerosols can be applied effectively only during very limited periods. Even at night, at least in those areas of Africa under the influence of the monsoons, atmospheric turbulence is often considerable, and, during daylight, inversions only exist for a short, variable, period of approximately 1 hour after dawn, and for a shorter and even more variable period of some 40 minutes before dusk. This limitation of the period during which aerosols can be effectively applied will have considerable bearing upon the economy of their use, particularly when aircraft are employed.

Evaporation Losses of Solvent.

The colorimetric assessments enabled deposits to be expressed in terms of volumes of original solution, whereas the size counts upon the oxide-coated plates gave the actual volumes of the deposits. Deposits at various positions relative to the aircraft track were assessed by both methods, and some idea of evaporation losses were obtained from the ratio

$$V = \frac{\text{cc. of original solution required to produce the deposit}}{\text{actual volume of the deposit in cc.}}$$

Thus V is unity when there are no evaporation losses.

The results are given in Table I. As before, time intervals were calculated from the mean wind speed at 5 m. and the distance downwind of the sample

TABLE I.

The ratio of the equivalent dosage of DDT, measured by the colorimetric method, to the liquid volume dosage measured upon glass plates coated with magnesium oxide.

Aircraft height (ft.)	Distance down-wind (yd.)	Time interval (sec.)	Volume per 100 drops (cc. × 10^{-6})	Mass median diameter (microns)	Ratio V	
30	0	(0)	9·4	78	2·3	=2·06
31	0	(0)	9·0	72	2·2	
30	0	(0)	21·0	101	1·6	
30	0	(0)	14·2	89	1·7	
77	0	(0)	8·2	82	2·4	
77	0	(0)	10·8	(87)	2·2	
30	15	3	7·0	75	2·1	=2·06
31	7·5	4	11·5	93	(1·3)	
30	12·0	9	14·2	89	1·8	
30	45	9	6·0	70	2·3	
70	35	15	9·2	79	2·5	
30	30	17	6·7	65	1·9	
31	30	17	6·5	71	2·5	
30	35	26	5·0	69	2·5	=2·30
30	75	43	5·1	53	1·7	
30	300	60	3·5	58	2·5	
31	130	72	4·4	64	2·3	
30	45	82	3·4	57	2·2	
30	130	98	3·7	64	2·5	
30	235	133	2·8	57	2·4	=2·53
31	130	167	2·9	55	2·5	
30	450	255	1·8	49	2·7	

Applying the correlation test to the time interval and V, the correlation coefficient $r = 0{\cdot}53$, and is significant.

from the line of emission; this gives zero time intervals for deposits formed immediately beneath the aircraft track, whereas in fact such deposits take a few seconds to form.

It is evident that the volume of a sample of 100 droplets decreases as the time interval increases, showing that the larger droplets are deposited more readily than the smaller droplets. The ratio V is approximately 2 for samples taken immediately beneath the aircraft track, so that droplets deposited within a very few seconds after their production have lost approximately 50 per cent. of their initial volume. A correlation test upon V and t showed that there was a significant increase in solvent losses with time, but the rate of increase was so slight that after 3–4 minutes the losses had only increased to 60 per cent. It seems likely that the relatively volatile power kerosene evaporates very rapidly during the first few seconds after production of the droplets, leaving droplets consisting of relatively involatile substances.

The data do not necessarily indicate that solvent losses are the same for all droplet sizes, and in fact there is some suggestion that for each group of data given in Table I evaporation losses are least with spectra consisting of larger droplets. A variation of 10 times in the droplet volume causes a variation of only 2·1 times in the droplet diameter, and this is approximately the limit of the variation in average droplet size of the spectra considered in Table I. The droplets in the aerosol varied in diameter from 5 microns to 250 microns approximately, and it is most probable that differences in evaporation losses occurred over such a wide range of sizes.

The evaporation losses will obviously depend upon the solvents. Some incomplete (unpublished) work showed that with a solvent consisting of 80 per cent. Shell Power Kerosene and 20 per cent. of the relatively involatile Shell Furnace Oil, evaporation losses were even greater than with the solvent used in these experiments, and that on the average approximately 70 per cent. of the solvent was lost; lubricating oils such as Shell S.A.E. 20, on the other hand, showed no measurable evaporation losses for time intervals and drop spectra similar to those given in Table I.

Although solvent losses do not involve losses of insecticide, they are to be avoided wherever possible. For any given application of insecticide, smaller variations in dosage are obtained if more droplets are used to produce the deposit, even if the solution strengths are reduced to maintain the same dosage of insecticide; this follows from the fact that in any small area the droplet numbers are distributed according to a Poisson series. It would therefore be preferable to use an involatile solvent, and produce more droplets, than to use a volatile solvent and produce more concentrated but fewer droplets of the same sizes.

The Dosages Received by an Insect.

An insect that is resting upon vegetation such as trees, or is flying, collects droplets in two ways; deposition by sedimentation upon horizontal surfaces, and deposition by impaction upon surfaces presented at right angles to the relative motion of the air mass. For flying insects the problem is greatly affected by the movement of the insect itself; the act of flying produces a complex form of relative air movement, and it is usually true that the dosages by impaction are very much greater than depositions obtained by sedimentation. For a stationary insect, however, it is possible to obtain general information upon the forms of these two deposits, if certain assumptions and simplifications are made.

The volume concentration in an aerosol cloud will vary with height, and with distance measured along the wind direction. In the following discussion, however, it will be assumed that, within a narrow layer of air just above the ground, aerosol concentration does not vary appreciably with height. It will also be assumed that there is only one size of droplet.

Let c be the concentration of aerosol per unit volume at some point within the narrow layer near the ground. Then a small volume, of unit cross sectional area at right angles to the wind direction and of length dl along the wind direction, contains an amount $c.\ dl$ of aerosol, and the amount of aerosol passing a unit vertical area placed at right angles to the wind direction is given by

$$\Sigma c.\ dl$$

where Σ denotes summation for all values of c. The summation may be called the *vertical area density*, and be denoted by C. The dosages received by an insect due to impaction can therefore be represented by the equation

$$\text{impacted deposit} = C.\Sigma(\mathrm{E}.\mathrm{A}_1) \quad \ldots \quad \ldots \quad \ldots \quad (6)$$

where E = efficiency with which the droplets impact upon an area A_1 exposed at right angles to the air flow, and Σ indicates the summation of all such terms. The efficiency of impaction depends complexly upon wind speed, droplet diameter, and the shape and size of the insect.

From an aerosol cloud of concentration c per unit volume an amount cV_s settles out on unit area in unit time, where V_s is the terminal velocity of the droplet. Thus the amount deposited from a small length of cloud dl is given by

$$c.dt.V_s = \frac{c.dl.V_s}{u}$$

since $dl = u.dt$, where u is the mean wind speed. The total sedimented deposit upon an insect is therefore given by

$$\text{sedimented deposit} = \frac{A_2 V_s \Sigma c.dl}{u}$$

$$= \frac{CV_s A_2}{u} \quad \ldots \quad \ldots \quad \ldots \quad (7)$$

where A_2 is the total horizontal area of the insect. Thus for a given value of C the relative importance of sedimentation, compared with impaction, decreases as the wind speed increases, particularly since E tends to increase with increasing wind speed.

In fig. 4 the proportion of DDT deposited within a time interval is plotted against time interval. Let P be this proportion for a time interval t; then the ground dosage can be represented by

$$\frac{1}{u}\frac{dP}{dt}$$

so that equations (6) and (7) may be written as

$$\text{impacted deposit} = \frac{1}{V_s}\frac{dP}{dt}\ \Sigma\,(E.A_1) \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (8)$$

$$\text{sediment deposit} = \frac{1}{u}\frac{dP}{dt} A_2 \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (9)$$

Thus, near the ground both sedimented and impacted dosages are proportional to $\frac{dP}{dt}$, values of which may be obtained from fig. 4. Taking the two extreme cases of $F = +\ 44 \times 10^{-3}$ and $F = -\ 34 \times 10^{-3}$, it is found that for time intervals up to 120 seconds, and almost certainly for greater intervals, $\frac{dP}{dt}$ is 3 to 4 times as great during strong inversions as during high superadiabatic lapse rates.

It does not necessarily follow that strong inversions and low wind speeds are always the most acceptable conditions for the applications of aerosols, even though such conditions will be always accompanied by the highest average ground dosages and vertical area densities. In practice it is necessary to treat an area by making a series of parallel runs spaced at intervals along the wind direction, and a case could arise, during inversions and low wind speeds, where, although the average dosages were very high, the wind speed would be so low that the aerosol from one run would not effectively reach downwind to the next run, and this would result in patchy areas where dosages would be slight. In our work, however, such occasions are extremely rare if the spacing between runs is of the order of 60 yd.

The above discussion applies only to a narrow layer of air near the ground surface. A full description of aerosol behaviour can be given only if the vertical area density at various heights above the ground, as well as the ground deposit, is studied in relation to variations in meteorological conditions, vegetation cover, and other variables. Furthermore, in woodland areas the dosages received by insects will be dependent upon their positions upon the vegetation; for example, insects resting upon the windward side of an obstacle will receive very different dosages from insects resting on the leeward sides.

Conclusion.

The data presented in this paper show that the deposition upon the ground of a coarse aerosol released from a low-flying aircraft is considerably affected by the degree of atmospheric turbulence, and that an adequate relation between the rate of deposition and atmospheric conditions may be obtained by taking relatively simple measurements of temperature gradient and wind speed. Increased turbulence, as measured by the factor F, decreases the rate at which the aerosol is deposited, and also, at least for the layer of air close to the ground, decreases the amount of aerosol available for impaction upon an insect that is resting upon vegetation such as trees. The experiments were, however, carried out under limited field conditions, and it is necessary to investigate the effect of changes in drop spectra, aircraft height, and the type and density of vegetation cover, before a more complete picture can be obtained of aerosol behaviour under practical field conditions. It is also important to investigate the variation with height of the density of the aerosol cloud. Experiments are being carried out in which it is hoped most of these factors will be studied in some detail.

Summary.

An investigation has been made of the deposition in open country of a coarse aerosol released from an aircraft flying at approximately 30 feet. A constant drop spectrum was used, with a mass median diameter of approximately 80 microns.

It is shown that the rate at which the aerosol deposits is greatly affected by the degree of atmospheric turbulence, a practical measure of which is described. The rate of deposition is approximately inversely proportional to the time interval elapsing between production of the aerosol and deposition, except for deposits laid down near the line of emission.

Droplets less than 10 microns in diameter are not deposited appreciably within any useful time interval, and it would be most uneconomical to attempt to produce deposits upon the ground by using drop spectra consisting mainly of such small droplets.

The solution used was a 10 per cent. w/v solution of technical DDT in a solvent consisting of 1 part of Shell Power Kerosene to 1 part of Shell Diesoline. Evaporation of the volatile constituents takes place very rapidly during the first few seconds after production of the droplets, and deposits formed immediately beneath the aircraft track have lost 50 per cent. of their initial volume. Solvent losses increase significantly with time, but so slowly that for most practical

purposes the solution strength of the ground deposit is very nearly constant for all important sampling points.

A general discussion is given of the dosages received by an insect, and it is indicated in a general fashion that in tropical Africa there are only short periods of daylight during which aerosols may be used most effectively.

The ground deposition in open country is only one aspect of the complex problem of aerosol behaviour, other important aspects of the problem are indicated.

Acknowledgements.

The authors are particularly grateful to Mr. K. S. Hocking, Officer in Charge of the Colonial Insecticides Research Unit, Arusha, who has been most helpful in planning the work, and to Dr. J. Robinson and Mr. E. T. Mesmer, who were burdened with large numbers of colorimetric estimations. To other colleagues, particularly Major G. C. Dauber, we are grateful for assistance in the onerous field work. We must also express our gratitude to the East African Meteorological Department and the Meteorological Section, Ministry of Supply, Porton, England, for advice and the loan of equipment. The flying was very satisfactorily carried out by pilots of Airwork Ltd.

The work has been financed by the Colonial Development and Welfare Fund, and has been directed by the Colonial Insecticides, Fungicides and Herbicides Committee.

References.

Best, A. C. (1935). Geophys. Mem., Lond., no. 65.

Calder, K. L. (1949). Quart. J. R. met. Soc., **75**, p. 71.

Deacon, E. L. (1949). *Ibid.*, p. 89.

Geiger, R. (1950). The climate near the ground.—Harvard Univ. Pr.

Gunn, D. L. & others. (1948*a*). Anti-Locust Bull., no. 4, 121 pp.

Gunn, D. L. & others. (1948*b*). Locust control by aircraft in Tanganyika.—153 pp., London, Anti-Locust Res. Cent.

Hocking, K. S. & Yeo, D. (1953). Bull. ent. Res., **44**, pp. 589–600.

Hesselberg, Th. & Björkal, E. (1921). Beitr. Phys. frei. Atmos., **15**.

Langmuir, I. & Blodgett, K. B. (1949). Rep. gen. elect. Res. Lab., no. R.L. 225.

May, K. R. (1945). J. sci. Instrum. **22**.

Richardson, L. F. (1920). Proc. roy. Soc., (A) **97**, pp. 354–373.

Richardson, L. F. (1925). Phil. Mag., **49**, pp. 81–90.

Scrase, F. J. (1930). Geophys. Mem., Lond., no. 52.

Sutton, O. G. (1949). Atmospheric turbulence.—London, Methuen.

STUDIES OF THE LIFE HISTORY AND ECOLOGY OF THE ANT *OECOPHYLLA LONGINODA* LATREILLE.

By M. J. Way.

*Clove Research Scheme, Zanzibar.** E.H.N.

(Plate VII.)

Of the five main subfamilies of ants, two, the Dorylinae and Ponerinae obtain almost all their food by predation, but the extent to which the remainder are predatory varies according to the species. Many obtain a proportion, and some all, of their food from other sources such as honey-dew-producing Homoptera (Nixon, 1951).

Attempts to control various insect pests of plants using predacious ants, which also attend Homoptera, have proved unsatisfactory (Bondar, 1922; Prell, 1925; Pickel, 1927; de Jong, 1944) because the Homoptera themselves became pests as a result of the benefits provided by the attendant ants. Nevertheless, species of *Oecophylla* have proved exceptional as beneficial predators. Friederichs (1920) mentions the 12th century southern Chinese practice of placing nests of *O. smaragdina* (F.) in citrus trees at the beginning of the fruiting season to control pests which would otherwise severely damage the developing fruit. *O. smaragdina* also protects mango fruit from damage by *Cryptorrhynchus* spp. (Curculionidae) (Friederichs, 1920; Voûte, 1935) and coconut palms from *Promecotheca* spp. (Chrysomelidae) (Friederichs, 1920; Murray, 1937). There is some evidence that Citrus trees (Groff & Howard, 1925; Garcia, 1939) and coconut palms (Simmonds, 1924) are protected by this ant from certain harmful Lepidopterous larvae.

O. smaragdina can control some Heteroptera, for example *Tessaratoma papillosa* (Dru.) (Groff & Howard, 1925) and *Rhynchocoris serratus* (Don.) (Garcia, 1935) on *Citrus* and *Amblypelta cocophaga* China on the coconut palm (Phillips, 1940; O'Connor, 1950). The closely related *Theraptus* sp. (Way, 1951, 1953*a*), which severely damages developing coconut fruits, is effectively controlled by *O. longinoda* (Latr.). In the Gold Coast, Strickland (1951) has demonstrated that this ant destroys Crematogasterine ants which attend the Pseudococcid vectors of swollen shoot disease of cacao; it tends Stictococcids which do not transmit this disease.

Oecophylla spp. have been considered harmful because they bite painfully and thus interfere with the harvesting of crops such as cloves, *Citrus*, coffee, rubber and lac. They also kill honey bees (Tryon, 1919) and benefit certain harmful Homoptera (Van Hall, 1922; Leefmans, 1934; Corbett, 1937), but their beneficial effect, notably in controlling coconut pests, sometimes outweighs these disadvantages.

Little is known of the biology of the genus *Oecophylla* except some details of nest-building habits and a study of *O. longinoda* was started in Zanzibar because it was found to attend the Coccid *Saissetia zanzibarensis* recently described by Williams (1953), which was thought might transmit sudden death disease of cloves (Nutman & Sheffield, 1949). It was observed (Way, 1951) that coconut palms occupied by the ant bore heavy crops of good nuts whereas neighbouring unoccupied palms bore small crops of severely damaged nuts. The damage, widespread in coconut-growing areas of British East Africa, was found to be caused by a Coreid, a species of *Theraptus*. This discovery made it desirable to study the biology of *O. longinoda* and its relationship with other insects, and with plants.

---

* Seconded from Rothamsted Experimental Station, Harpenden.

Distribution of *Oecophylla* Species.

The genus *Oecophylla* occurs in tropical Asia, Australasia and Africa. Varieties of the species *O. smaragdina* have been recorded in southern India, Ceylon, Burma, Malaya and in countries and islands lying between and including south China and North Australia. *O. longinoda*, of which there are five varieties (Wheeler, 1922), is the African representative of the genus.

In British East Africa, *O. longinoda* is most abundant in the area of forest vegetation along the coasts of Kenya and Tanganyika and on the islands of Pemba, Zanzibar and Mafia, where temperature and rainfall are higher than inland and diurnal and seasonal variation are less pronounced (Table I—Mombasa and Zanzibar). Where the soil is suitable, the evergreen tree and bush vegetation is rich throughout the year; probably this is essential for the maintenance of *O. longinoda* colonies, which use the living leaves of trees for their nests and also depend on certain plant-feeding Homoptera for much of their food.

In inland areas of Kenya and Tanganyika, particularly at higher altitudes, *O. longinoda* is uncommon or absent (R. H. Le Pelley, priv. comm., and personal observation). The temperature here is lower, diurnal variation is considerable, rainfall is generally lower and there is often a well-defined dry season (Table I—Nairobi and Iringa). The vegetation also is less well developed; some trees are deciduous, or show xeromorphic characters, and thus are probably useless for nest construction by the ant. Lack of suitable host trees is apparently not the sole cause for the absence of *O. longinoda*, because in the Lyamungu area there is a rich forest vegetation. The relatively low temperatures (Table I) and pronounced diurnal variation may prevent colonisation by *O. longinoda*.

In Uganda, *O. longinoda* has been recorded from at least two areas—islands in Lake Victoria (Carpenter, 1920) and in the region of Lake Albert (A. P. G. Michelmore, priv. comm.), where there is a high rainfall distributed throughout the year, and a tropical or sub-tropical vegetation (Table I—Entebbe). However, the altitude is such that the mean temperature is about 10°F. lower than in the coastal region.

In the Zanzibar Protectorate, *O. longinoda* occurs as the variety *textor* Santschi. It is not found in certain areas of thin soil overlying porous coral rock where the conditions are such that tree and bush vegetation is sparse or

TABLE I.

Distribution of *O. longinoda* in East Africa in relation to climate.

Locality		Height (ft.)	Total rainfall (in.)		Annual temperature (°F.)	
			Nov.–May	June–Oct.	Mean max.	Mean min.
O. longinoda present	Mombasa	52	30·8	17·0	86·1	74·2
	Zanzibar	18	52·4	11·7	86·4	74·1
	Entebbe	3878	41·8	17·4	78·2	63·4
O. longinoda absent	Nairobi	5971	31·2	6·7	74·0	54·5
	Iringa	5330	30·4	0·4	75·9	56·6
	Lyamungu*	4400	69·3	13·0	75·9	57·8

Data from mean of 10–15 years' records (Matheson & Bovill, 1950), except *, which is mean of 3 years' records (1936–38) obtained from Tanganyika Dept. Agric. annual reports.

non-existent. Elsewhere in the Protectorate there is usually a rich vegetation and the ant is locally abundant, but its distribution and abundance are influenced largely by three other ant species which have replaced it or dominate it in certain areas (Way, 1953*b*).

Castes of *O. longinoda.*

The castes of *O. longinoda* var. *textor* are easily differentiated into small and large workers, males and females. In the field, the small workers (fig. 1,*b*) are

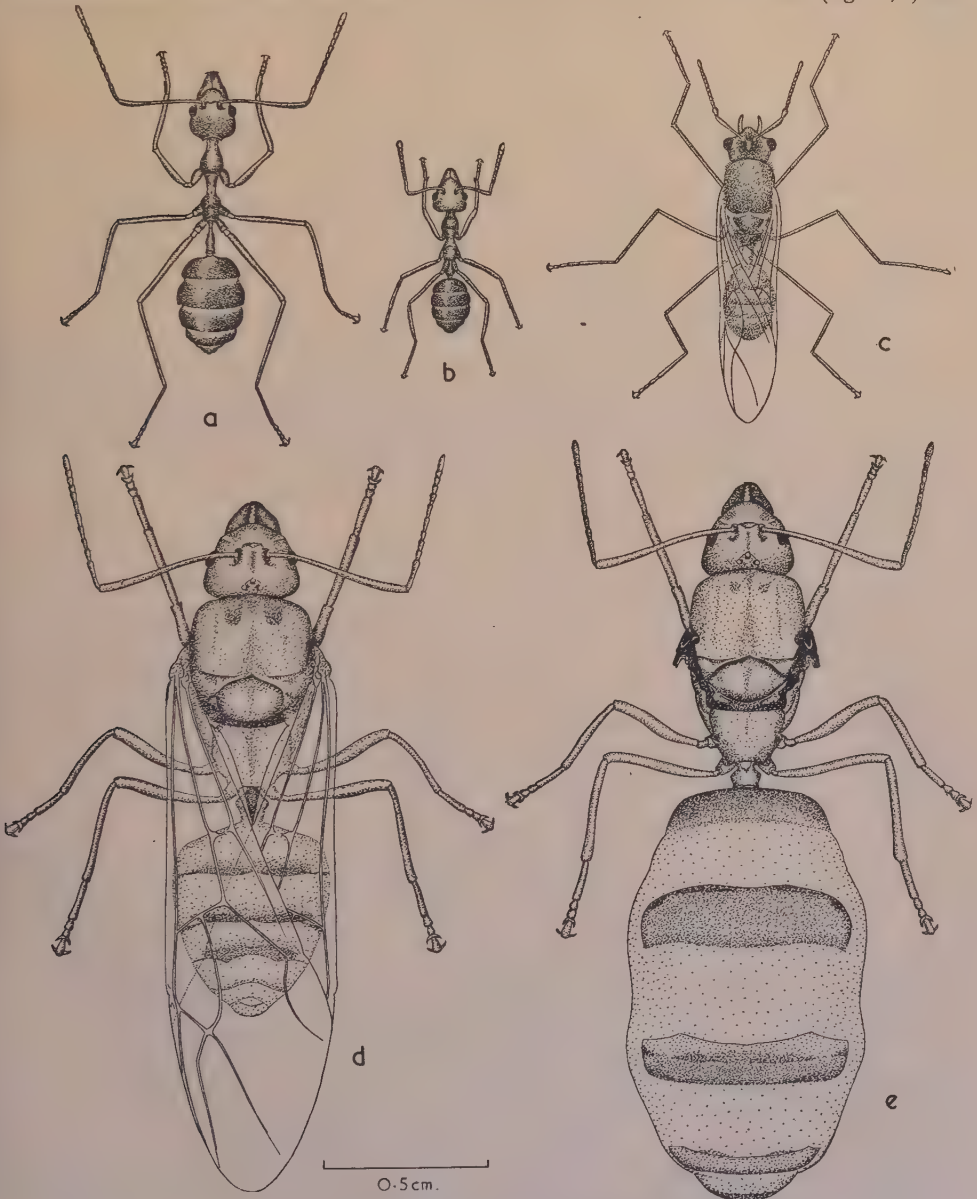


Fig. 1.—Castes of *O. longinoda* var. *textor*: *a*, large worker; *b*, small worker; *c*, male; *d*, virgin female; *e*, gravid queen.

seldom found outside the immediate proximity of the nests; they may solicit honey-dew-producing Homoptera within the nests, but otherwise their main function is to attend the developing brood and the sexual forms. The large workers (fig. 1,*a*) attend honey-dew-producing Homoptera outside the nests, forage on the ground, kill other insects for food, and defend the colony. They are almost the only form that builds nests and shelters over clusters of Homoptera; they also attend the brood and carry it from nest to nest within the colony. Table II shows the proportions of adults and pupae of the two forms of workers in five medium to large nests from three different *O. longinoda* colonies on the clove tree.

TABLE II.

Numbers of adults and pupae of large and small workers in nests of *O. longinoda*.

Nest no.	Large worker adults	Small worker adults	Large worker pupae	Small worker pupae	Other brood
1.	1165	1082	967	715	2227
2.	2203	5374	1563	1081	88
3.	6827	11838	1063	628	11209
4.	5574	5285	270	24	13182
5.	4614	7624	3262	1958	1612

It will be noticed that, although the pupal counts show that more large workers are produced than small, more small workers than large occur within the nests. This is because many large workers are foraging outside.

The virgin sexual forms of *O. longinoda* are illustrated in figs. 1,*c*,*d*. The gravid queen (fig. 1,*e*) is dealated and has an abdomen greatly distended with developing ova.

Nesting Habits of *O. longinoda*.

O. longinoda, like *O. smaragdina*, builds arboreal nests and has never been observed to nest or even forage beneath the soil surface. In Zanzibar it has been found colonising some 89 species of trees and shrubs belonging to 35 families, a list of those which were identified being given in Table III. Grateful acknowledgement is due to the Director of the Royal Botanic Gardens, Kew, for correcting the plant names. For some species whose names have recently been changed the original name is given in brackets.

TABLE III.

Incomplete list of species of Homoptera tended by *O. longinoda* on various host plants in Zanzibar Island.

Host plant	Species tended by *O. longinoda*
ANACARDIACEAE	
Anacardium occidentale	*Pseudococcus* sp., *Coccus* sp. nr. *hesperidum* L., *Saissetia zanzibarensis* Williams, *Saissetia nigra* (Nietn.)
Mangifera indica	*Pseudococcus* sp., *Phenacoccus iceryoides* Green, *C. hesperidum*, *S. zanzibarensis*, *Saissetia* sp. nr. *nigra*.
ANNONACEAE	
Annona chrysophylla	*Saissetia* sp. ?*nigra*, *Isthmia* sp. (TETTIGOMETRIDAE).
Annona muricata	*Saissetia* sp. nr. *nigra*, *Stictococcus anonae* Green & Laing.
Canangium odoratum	*Stictococcus anonae*.
APOCYNACEAE	
Rauwolfia mombasiana	*Pseudococcus* sp., *Coccus viridis* (Green), *Saissetia* sp. nr. *coffeae* (Wlk.), *Saissetia* sp. nr. *catori* (Green).
Schizozygia coffeoides	*P. iceryoides*, Membracid sp.

Host plant	Species tended by *O. longinoda*
BIGNONIACEAE	
Millingtonia hortensis	*Saissetia* sp. nr. *catori*.
BOMBACACEAE	
Adansonia digitata	*S. zanzibarensis*, Margarodid sp., *Saissetia* sp. nr. *catori*.
Durio zibethinus	*Coccus* sp. nr. *elongatus* (Sign.), *Saissetia* sp. nr. *catori*.
BURSERACEAE	
Canarium commune	*S. zanzibarensis*, Membracid sp.
COMBRETACEAE	
Terminalia catappa	*Saissetia* sp. Membracid sp.
COMPOSITAE	
Ageratum sp.	*Pseudococcus* sp., *Saissetia* sp. nr. *nigra*.
CUCURBITACEAE	
Momordica foetida	*Saissetia* sp. nr. *coffeae*.
EUPHORBIACEAE	
Bridelia micrantha	*S. nigra*, Membracid sp.
Codiaeum sp.	*Pseudococcus* sp.
HYPERICACEAE	
Harungana madagascariensis	*Pseudococcus* sp., *C. viridis*, *S. zanzibarensis*, *Saissetia* sp. nr. *nigra*, *Xiphistes* sp. (MEMBRACIDAE).
LAURACEAE	
Cassytha filiformis	*Saissetia* sp. nr. *oleae* (Bern.).
Persea americana	*C. hesperidum*, *S. zanzibarensis*.
LECYTHIDACEAE	
Barringtonia racemosa	*Coccus* sp. nr. *elongatus*, *Saissetia* sp. nr. *nigra*, Membracid sp.
LEGUMINOSAE	
Bauhinia thonningii	*C. hesperidum*, *S. zanzibarensis*, Membracid sp.
Cassia sp.	*S. zanzibarensis*, Membracid sp.
Delonix regia	*S. nigra*.
Gliricidia sepium	*P. iceryoides*, *S. zanzibarensis*.
Leucaena glauca	*C. hesperidum*.
Pithecollobium dulce	Membracid sp.
Tephrosia vogelii	*C. hesperidum*.
LILIACEAE	
Gloriosa simplex	*S. zanzibarensis*.
LORANTHACEAE	
Loranthus sansibarensis	*Saissetia* sp.
MALVACEAE	
Malvaviscus grandiflorus	Coccid sp.
MORACEAE	
Artocarpus heterophyllus	*C. hesperidum*.
Ficus spp.	*P. iceryoides*, *S. zanzibarensis*, *S. nigra*, Margarodid sp.
MYRTACEAE	
Eucalyptus camaldulensis	*Coccus* sp. ?*hesperidum*, *C. viridis*, *S. zanzibarensis*.
Jambosa caryophyllus (*Eugenia aromatica*)	*Coccus* sp. nr. *hesperidum*, *C. viridis*, *Eulecanium* sp., *S. zanzibarensis*, *Saissetia* sp. nr. *coffeae*, *Saissetia* sp. nr. *nigra*.
J. jambos (*E. jambos*)	*Coccus* sp. nr. *hesperidum*, *Eucalymnatus tessellatus* (Sign.), *S. zanzibarensis*, Membracid sp.
J. malaccensis (*E. malaccensis*)	Membracid sp.
Psidium guajava	*Pseudococcus* sp., *C. viridis*, *S. zanzibarensis*.
Syzygium cumini (*E. jambolana*)	*Coccus* sp. nr. *viridis*, *S. zanzibarensis*, Membracid sp.
OLEACEAE	
Jasminum fluminense	*S. zanzibarensis*.
OXALIDACEAE	
Averrhoa bilimbi	Pseudococcid sp., *S. zanzibarensis*.
A. carambola	*S. zanzibarensis*.

Host plant	Species tended by *O. longinoda*
PALMAE	
Areca catechu	*S. zanzibarensis.*
Cocos nucifera	*Cerataphis lataniae* Boisd., *Steatococcus* sp., *Pseudococcus citriculus* Green, *Planococcus* sp., *C. hesperidum, S. zanzibarensis, S. nigra.*
PASSIFLORACEAE	
Passiflora quadrangularis	*S. nigra.*
RHAMNACEAE	
Ziziphus mauritiana	Pseudococcid sp.
RHIZOPHORACEAE	
Ceriops sp.	*S. zanzibarensis, S. nigra.*
Rhizophora mucronata	*S. zanzibarensis.*
ROSACEAE	
Eriobotrya japonica	Coccid sp.
RUBIACEAE	
Canthium zanzibaricum	*Pseudococcus* sp., *C. hesperidum, S. zanzibarensis, Saissetia* sp. nr. *nigra.*
Chasallia umbraticola	*C. viridis.*
Coffea excelsa	*C. viridis, S. zanzibarensis.*
C. liberica	*C. viridis, S. zanzibarensis, S. nigra.*
C. robusta	*C. viridis, S. zanzibarensis.*
Polysphaeria sp.	*C. viridis.*
RUTACEAE	
Citrus, five spp.	*Cerataphis lataniae, Icerya seychellarum* (Westw.), *Planococcus citri* (Risso) *Pseudococcus citriculus, Pseudococcus* sp., *C. hesperidum, C. viridis, S. zanzibarensis.*
Murraya paniculata	Coccid sp.
SAPINDACEAE	
Nephelium lappaceum	*C. hesperidum, Saissetia* sp. nr. *catori, S. anonae.*
Paullinia pinnata	Pseudococcid sp.
SAPOTACEAE	
Achras zapotilla	*C. viridis, S. zanzibarensis, Saissetia* sp. nr. *coffeae.*
SONNERATIACEAE	
Sonneratia alba (*S. caseolaris*)	*S. nigra, Saissetia* sp. nr. *oleae.*
STERCULIACEAE	
Theobroma cacao	*Toxoptera* sp. ? *aurantii* (Boy.), *Pseudococcus* sp., *P. iceryoides.*
TILIACEAE	
Grewia glandulosa	*P. iceryoides*, Margarodid sp.
VERBENACEAE	
Clerodendron glabrum	*S. zanzibarensis.*
Tectona grandis	*C. hesperidum*, Membracid sp.
Vitex doniana	*C. hesperidum, Saissetia* sp. nr. *coffeae.*

Insects recorded as *Pseudococcus* sp. and *Saissetia* sp. are probably distinct species, hitherto undescribed.

The plants which, relative to their size, supported the heaviest ant populations were *Bridelia micrantha* and the clove, *Jambosa caryophyllus*. *Citrus* species, *Canthium zanzibaricum* and *Coffea liberica* were also favoured host plants. In Tanganyika and Kenya thriving colonies of *O. longinoda* were observed on cashew (*Anacardium occidentale*). The choice of host plant appears to depend partly on the ease with which the leaves can be used to form nests, and partly on the ability of the host plant to support suitable Homoptera from which the ant can obtain honey-dew for food. *O. longinoda* has not been observed nesting in *Artocarpus communis*, the leaves of which are large and relatively inflexible but it can adapt the foliage of most trees for nest-building. Large nests consisting of hundreds of leaves may be built in trees such as the clove, which produces a thick growth of simple leaves about 3½ in. long (Pl. VII, figs. 1 & 4). In trees such as cacao, *Theobroma cacao*, up to about ten of the relatively large leaves may be drawn together, while single large (16 in. long) simple leaves of *Barringtonia racemosa*, or single pinnate leaves of *Delonix regia* are sometimes curled over and the leaflets pulled together to form nests. On the coconut palm, *Cocos nucifera*, several leaflets of a frond are drawn across each other and the exposed undersides of the leaflets, which are ∧-shaped in cross section, are covered with a mesh of silk (Pl. VII, fig. 2). On *Murraya paniculata* the leaves are often too small to enclose a nest, and quantities of dead leaves and stems may be collected and included in the nest structure; on *Leucaena glauca*, nests are sometimes made from groups of developing fruit bound together with silk.

The process of nest-building or of repairing damaged nests by *Oecophylla smaragdina* has been briefly described by Ridley (1890), Dodd (1902), Doflein (1905) and Hingston (1927). Observation of *O. longinoda* colonies on the clove tree showed that, about a day before starting to build, the larger workers crawled slowly over the nest area. As a result of this examination the ants seem to determine whether there are leaves enough to form a nest. The larger workers then began to draw individual leaves together, sometimes forming chains of up to twelve workers to bridge the gaps. The chains are formed by each ant gripping with its mandibles the very long petiole of the ant in front and the leaves are gripped by the mandibles and by the well-developed tarsal claws. On the coconut palm about two hundred workers in chains of up to nine individuals were observed drawing a pair of leaflets together and the manner in which all chains co-ordinated in pulling together was most striking. Leaves were

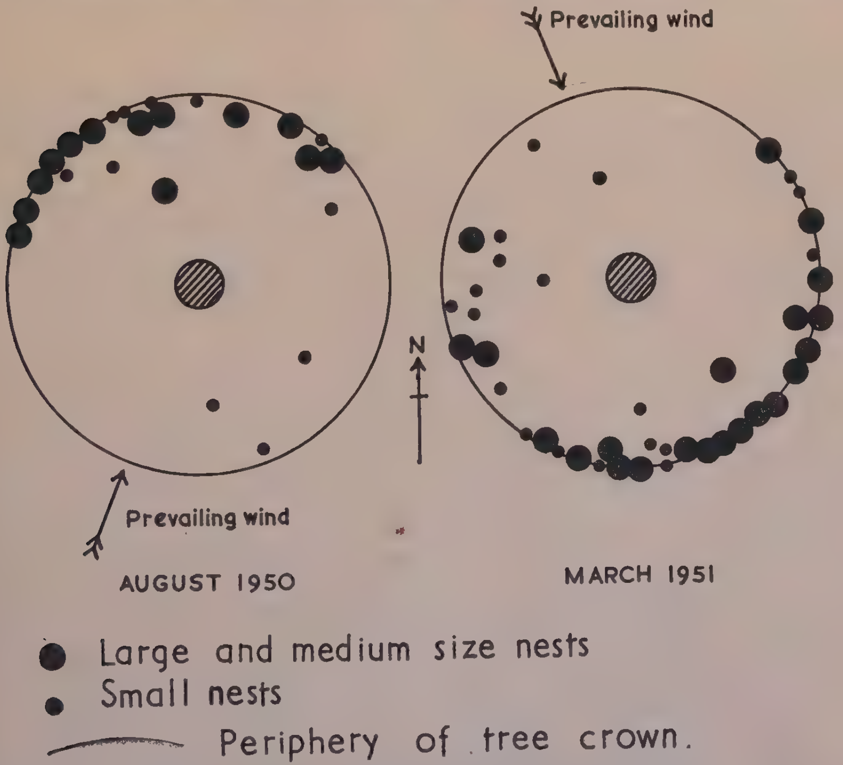


Fig. 2.—Diagrammatic composite plan showing the seasonal variation in position of nests of a colony of *O. longinoda* covering five clove trees.

occasionally rearranged on clove trees and then drawn together in a different and apparently more convenient position, indicating that the process of nest-building is highly organised. After the leaves had been drawn together, they were held in position by workers, while others, carrying medium-sized larvae in their mandibles, proceeded to secure the edges together with silk secreted by the larvae (*cf.* Ridley, 1890; Doflein, 1905). Small shelters of three to four leaves, or of silk mesh alone, are built in a similar way over clusters of Homoptera on which the ant is attendant. Such shelters are not considered to be nests because they do not contain brood.

A colony of *O. longinoda* on five small clove trees was observed for five months (10.viii.50–15.i.51). There were twenty-four nests at the start and thirty-three at the end. An average of nine nests was built each calendar month, each of which was occupied for an average of eighty-five days and deserted when most of the leaves of which it was built had died.

The part of the tree selected for nest-building varied according to the season, as shown in fig. 2.

The variation seemed to be correlated with wind direction. From about December to April the monsoon blows consistently from the north-east, and from the south-east during about May to November. Fig. 2 shows that nests of *O. longinoda* occurred mainly on the sheltered side of the tree; this may be because it is more difficult to build when leaves are being disturbed by the wind, and also because the sheltered side of the tree is the one which receives most radiant heat from the sun. The tendency to construct nests on slopes facing the sun has been observed also with certain soil-nesting ant species and probably affects the rate at which the insect develops.

Composition of *O. longinoda* Colonies.

In areas occupied by *O. longinoda*, well-defined paths over fallen branches and fronds were used by the workers to connect neighbouring trees that contained nests, indicating that a single colony may occupy several trees. Maps were made showing the positions of trees connected in this manner.

Fig. 3 shows that the colonies did not overlap; several experiments, both in the field and nursery, showed that mature workers from different colonies are antagonistic.

The nests from ten colonies were counted and their contents examined (Table IV). Eggs, larvae and pupae often occurred in the same nest, and nests

TABLE IV.

Details of *O. longinoda* colonies examined in the field.

No. of colony	No. of trees comprising colony	Total *O. longinoda* nests per colony	No. of gravid queens per colony
1	1 (Clove)	5	1
2	6 (Clove)	29	1
3	1 (Coconut)	49	1
4	1 (Coconut)	38	0
5	3 (Coconut)	38	0
6	10 (Coconut)	44	1
7	4 (*Harungana madagascariensis*)	21	1
8	4 (2 Clove, 2 *Citrus*) ..	88	0
9	9 (3 Clove, 6 coconut) ..	106	1
10	12 (8 Clove, 4 coconut) ..	151	1

on all trees within the colony usually contained brood of all ages but only one gravid dealated queen was found in each colony. She was always in a small nest from which worker ants carried batches of eggs along the pathways to other nests within the colony.

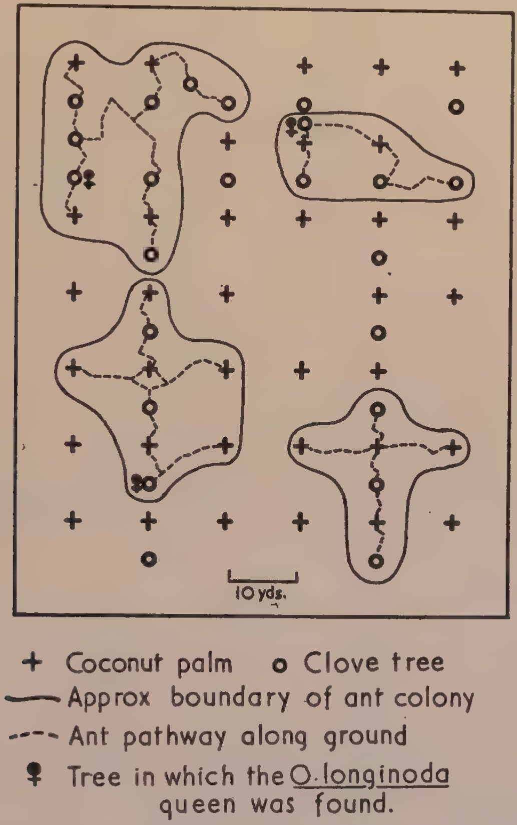

10 yds.
+ Coconut palm
o Clove tree
—— Approx boundary of ant colony
---- Ant pathway along ground
♀ Tree in which the O. longinoda queen was found.

Fig. 3.—Plan of part of a clove-coconut plantation showing the position of four colonies of *O. longinoda.*

The population was roughly estimated by counting the numbers of workers and ant brood in nine nests on clove trees and nine nests on coconut palms from colony no. 10 (Table V).

It was then calculated that colony no. 10, comprising twelve trees containing 151 nests and covering an area of about 1/5 acre, contained a total population

TABLE V.

Mean numbers of workers and brood of *O. longinoda* within nests built on coconut palms and in clove trees (colony no. 10).

Tree	No. of nests examined	Mean no. workers per nest	Mean no. brood per nest
Coconut	9	719	298
Clove	3 (small) ..	707	238
	3 (medium) ..	4994	4336
	3 (large) ..	13383	8981

within nests of about 480,000 workers and 280,000 brood. These figures should be treated with reserve because they are based on relatively few quantitative data. It should also be noted that they do not include the large number of worker ants outside the nests at the time of collection.

Production of Sexual Forms by *O. longinoda* Colonies.

Nests were examined, at intervals from August 1950 to December 1951, for the presence of virgin sexual forms. In August and September 1950, few virgin winged male and female adults were found, generally no more than two to three in a nest. Most nests contained only worker adults and brood, though perhaps some of the young larvae were sexual forms. In October 1950, up to 35 queen larvae and pupae were observed in some nests, as well as small numbers of male and female adults, and male pupae. Immature and adult sexual forms became increasingly frequent during the following four months and, in February 1951, 235 mature virgin females were counted in one nest and 418 males in another. Both sexes were sometimes found in the same colony at the same time, but seldom in the same nest. Moreover, detailed examination of two colonies showed that one contained females and very few males, while the other contained only males. This suggests that a colony may tend to produce only one sex at any one time but this point requires further investigation.

Between 26th February and 23rd March 1951, dealated females were found on vegetation in the field, and flying females, attracted by lights at night, were caught in houses in Zanzibar town. In March 1951, only brood and a few immature adults of sexual forms were found in the nests examined, indicating that the mature forms had been released during the end of February and beginning of March 1951.

In April 1951, a few mature sexual forms were again found in nests, but at the beginning of May a dealated queen was found on vegetation in the field and no mature sexual forms remained in the nests. From August 1951 onwards, mature sexual forms and brood were again observed in nests, and at the beginning of October 1951 these were released. Again, between 11th October and 19th October, a number of released queens was found.

The release of winged sexual forms always coincided with the beginning of periods of prolonged high humidity and frequent rainfall (see fig. 4).

The wet season at the end of 1950 was not well defined. Release of virgin sexual forms was not observed at this time, perhaps because the conditions of rainfall and humidity were unsuitable. In October and November 1951, there was a well defined wet season (fig. 4) and sexual forms were released.

In general these observations agree with those of Wigg (1936) who, as a result of several years' observations, showed that adult sexual forms occurred within nests only during the period October to May.

Colony Formation by *O. longinoda*.

Five dealated and two alate queens of *O. longinoda* collected after the mating flight, were each placed in a small chamber composed of 3–4 leaves of a potted clove seedling loosely tied together. The aerial parts of the plants were sprayed daily with water but no food was provided. The alate queens cast their wings and all settled down in the chambers.

A record of the progress of one queen was as follows:—

26.ii.51.	Queen collected in field and placed in chamber.
2.iii.51.	Packet of eggs observed.
13.iii.51.	More eggs laid, some hatched.
25.iii.51.	Queen had used some larvae to spin webs of silk across entrance to chamber.

4.iv.51. Two worker ants emerged—intermediate in size between small and large workers.

11.iv.51. Nine workers emerged. None observed foraging outside chamber. Drops of honey placed on plant near chamber and nymphs of *Saissetia zanzibarensis* established on plant to provide honey-dew for colony.

12.v.51. About thirty workers present. Leaves comprising chamber strongly bound together with silk. Entrance to chamber covered by thick web of silk except for one small opening to allow passage of workers. Workers soliciting *S. zanzibarensis* for honey-dew. Quantities of eggs and brood present in chamber.

It should be noted that, until mature workers were produced, the queen used only her food reserves to feed the developing brood.

Of the seven queens collected, two died without laying eggs, two laid eggs but died before workers were produced, and the others established colonies as described above.

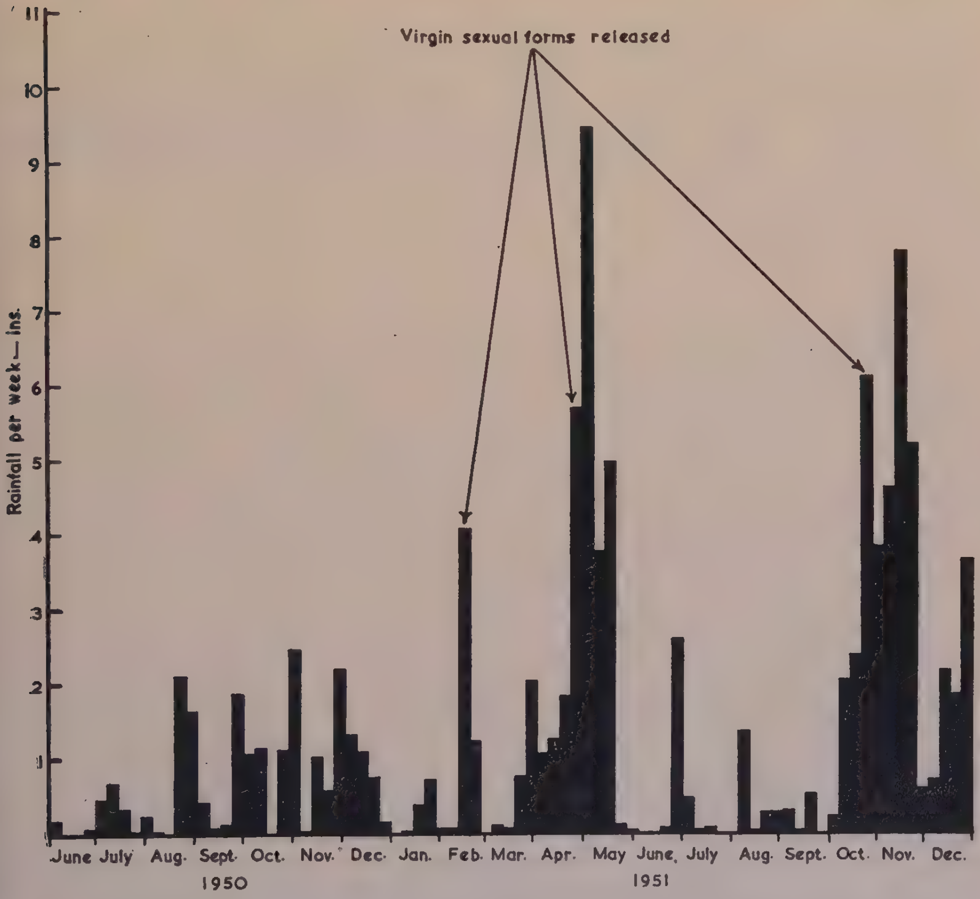


Fig. 4.—Weekly rainfall figures for Zanzibar (Victoria Gardens) during 1950–51 showing times of release of virgin sexual forms of *O. longinoda*.

Longevity of *O. longinoda* Colonies.

The evidence presented above shows that only one fertile queen is present in each colony, and it is not known whether, if the queen dies, such a colony would accept a young queen newly returned from the mating flight.

On several occasions when trees which contained nests but no queen were deliberately isolated from the rest of the colony, the ants eventually died out; also in nursery experiments with artificially established colonies, queenless colonies died out unless brood was added from time to time. In a further experiment, batches of the *O. longinoda* nests, several of which contained virgin males and females, were placed in each of forty-eight coconut palms. The ants became established in most of the trees but, after a year, all the colonies had died out except two which were flourishing. One contained an old queen which had probably been present in the introduced nests, the other contained brood of all ages, although the queen was not found.

These results may suggest that, in the absence of a fertile queen, neither virgin sexual forms nor workers can reproduce.

Relations of *O. longinoda* with Honey-Dew-Producing Homoptera.

Colonies of *O. longinoda* are always associated with certain Homoptera from which they obtain honey-dew. Although *O. longinoda* is predatory on other insects, these are a relatively minor source of food supply, and honey-dew-producing Homoptera are apparently essential for survival (Way, 1954). Studies on the Coccid, *Saissetia zanzibarensis*, commonly associated with *O. longinoda*, have shown that this insect receives much benefit from the ant (Way, 1954). Furthermore, within an ant colony, the Coccid population is maintained at a level adequate for the honey-dew requirements of the colony.

The species of Homoptera which were found being attended by the ant are listed in Table III. Some appear to be new species which have not yet been described.

Several points are worthy of note:—

(a) Coccids, particularly *Saissetia* spp., and, to a less extent, *Coccus* spp. were the most widespread and abundant of the Homoptera attended by *O. longinoda*. The most dense populations of *O. longinoda* occurred on the clove and on *Bridelia micrantha* and were always associated with similarly dense populations of *Saissetia* spp. Dense populations of the ant associated with *S. zanzibarensis* were also seen on *Canthium zanzibaricum* and *Citrus*. *S. zanzibarensis* attended by *O. longinoda* was found on thirty species of host plants. Also, the following species attended by the ant were recorded on one *Citrus* tree:—*S. zanzibarensis*, *C. hesperidum* L., *C. viridis* (Green), *Pseudococcus citriculus* Green and *Icerya seychellarum* (Westw.).

(b) *O. longinoda* was found attending a Stictococcid on three different host plants but not on cacao (*Theobroma cacao*) (*cf.* Strickland, 1951).

(c) Pseudococcids tended by *O. longinoda* were found in relatively small numbers except on cacao where clusters of several hundred individuals of *Pseudococcus* sp.* were sometimes found causing damage to developing fruit (Pl. VII, fig. 3). *O. longinoda* was not observed to attain a dense population when only Pseudococcids were present.

(d) The Aphid, *Cerataphis lataniae* Boisd., was often attended by *O. longinoda* on the coconut palm and occasionally on *Citrus* spp. Twice the ant was observed soliciting small clusters of the Aphid, *Toxoptera* sp. ?*aurantii* (Boy.), once on cacao and once on an unidentified plant.

(e) Small numbers of nymphal and adult Membracids (including *Xiphistes* sp.) on ten different species of trees and shrubs, and *Isthmia* sp. (Tettigometridae) in large numbers on developing fruit on *Annona chrysophylla* were also found in association with *O. longinoda*.

---

* This appears to be an undescribed species which does not belong to the genus *Pseudococcus* as at present understood.

Thus the ant can use a wide range of Homoptera and this may be important in connection with colony formation by young queens. Bunzli (1935) has shown that virgin females of the ant *Acropyga paramaribensis* Borgm. carry young female Coccids on their mating flight, which are presumably used to provide honey-dew when the queen establishes a colony. Queens of *O. longinoda*, captured after the mating flight, have not been observed to carry Homoptera, and the problem, presented to the first worker ants, of finding a suitable species is simplified by the wide range of Homoptera they can use.

Choice of Honey-Dew-Producing Homoptera by *O. longinoda*.

A careful search was made for Homoptera on the clove tree (*Jambosa caryophyllus*) and a record made when these were tended by any of the three most common ant species in Zanzibar, *O. longinoda*, *Anoplolepis longipes* (Jerd.) and *Pheidole punctulata* Mayr.

Table VI shows that six species of Homoptera, all Coccidae, were attended by *O. longinoda* on the clove. Certain other Homoptera, however, were often found on the clove and other trees occupied by the ant but these species, *Coccus acuminatus* (Sign.), *C. bicruciatus* (Green) and *Ceroplastes rubens* Mask., were not attended although they produce honey-dew, and *A. longipes* and *P. punctulata* have been observed collecting it (see Table VI). This suggests "choice" of particular honey-dew-producing Homoptera by the ant.

TABLE VI.

Observations on ant solicitation of Homoptera found on the clove tree.

Species of Homoptera	Solicited by			Found in absence of ants
	O. longinoda	*A. longipes*	*P. punctulata*	
Margarodidae				
Icerya seychellarum (Westw.)			Yes	Yes
Pseudococcidae				
Pseudococcus adonidum (L.)				Yes
Paraputo ritchiei Laing			Yes	
Coccidae				
Coccus acuminatus (Sign.)		Yes		Yes
Coccus sp. ? *africanus* (Newst.)		Yes	Yes	
C. bicruciatus (Green)		Yes	Yes	Yes
Coccus sp. nr. *hesperidum* L.	Yes			
C. viridis (Green)	Yes	Yes*		
Eulecanium sp.	Yes			
Saissetia zanzibarensis Williams	Yes			
Saissetia sp. nr. *coffeae* (Wlk.)	Yes			
Saissetia sp. nr. *nigra* (Nietn.)	Yes			
Saissetia sp. ? *oleae* (Bern.)		Yes*		
Eucalymnatus tessellatus (Sign.)		Yes	Yes	Yes
Pulvinaria psidii Mask.				Yes
Ceroplastes rubens Mask.		Yes	Yes	Yes
Ceroplastes ceriferus (And.)			Yes	Yes
Vinsonia stellifera (Westw.)				Yes
Diaspididae				
Chrysomphalus dictyospermi (Morg.)				Yes
Hemiberlesia palmae (Ckll.)				Yes
Parlatoria proteus (Curt.)				Yes

* A single individual found once only.

The characteristics which apparently render species of Homoptera acceptable to ants are:—

(a) High fecundity and rapid rate of reproduction.
(b) Ability to excrete much honey-dew. This would probably be directly related to (a).
(c) Ability to feed on a wide range of host plants.
(d) Clustering habit.
(e) Ability to thrive in the absence of attendant ants. This requires amplification:—Homoptera may benefit in two important respects from attendance by ants. First from general attention such as removal of honey-dew and transport to suitable feeding sites, and secondly from protection against parasites and predators. In extreme cases, the Homoptera species are virtually dependent on close association with the ant. Thus in Zanzibar *S. zanzibarensis* was rarely found and *S. nigra* (Nietn.) never found in the absence of *O. longinoda* (Way, 1954).

Homoptera such as *S. zanzibarensis* and *S. nigra* cannot be used by ant species which provide less efficient attention than *O. longinoda*. Such ants can only use species which although less suitable in some respects have the advantage of being more independent of ant attendance. For example, in trees, heavy populations of *A. longipes* and *P. punctulata* were associated with the presence of Pseudococcids, especially *Phenacoccus iceryoides* (Green), and the Aphid *Cerataphis lataniae* Boisd., which appear to be more independent of ant attention than are the *Saissetia* spp.

The selection of Homoptera by ants has recently proved economically important with swollen shoot disease of cacao in West Africa. Strickland (1951) has shown that on cacao the population density of *Pseudococcus njalensis* Laing, the vector of swollen shoot, is correlated with the presence of attendant Crematogasterine ants. The presence of *P. njalensis* is negatively correlated with the ant *O. longinoda*, which is highly correlated with the presence of Stictococcids, notably *Stictococcus sjostedti* Ckll. which, like *Saissetia zanzibarensis* in Zanzibar, nearly always occurs only in association with *O. longinoda*. It seems that Crematogasterine ants, unlike *O. longinoda*, do not benefit Stictococcids adequately and thus have become adapted to utilising the otherwise less suitable *P. njalensis* as a source of honey-dew. The last-named species has the disadvantage of a relatively low biotic potential, but it can thrive independently of ant protection, for under laboratory conditions it reached far higher populations in the absence, than in the presence of attendant ants (Strickland, 1947). This is in direct contrast to the behaviour of *S. zanzibarensis* (Way, 1954). In Zanzibar, neither Coccids nor Stictococcids have been recorded on cacao and therefore, on this host plant, *O. longinoda* can only attend the apparently less suitable Pseudococcids, *Pseudococcus* sp. (Pl. VII, fig. 3) and *Phenacoccus iceryoides*.

Predation by *O. longinoda*.

Reference has already been made to reports which show that *Oecophylla* species prey on certain pests. In Zanzibar, large workers of *O. longinoda* forage on the ground and over trees and shrubs and attack most insects with which they come in contact, notable exceptions being three other ant species which are themselves aggressive towards *O. longinoda* (Way, 1953*b*). *O. longinoda* workers do not interfere with certain Lepidopterous larvae predatory on the ant-attended Homoptera (Way, 1954) nor with a species of spider which mimics the ant. Also they do not react to, or appear to notice, small insects of about 1 mm. or less in length, for example, adults of certain CECIDOMYIIDAE, ENCYRTIDAE parasitic on Coccids, *Ctenarytaina* sp. (PSYLLIDAE) which attack the young growing points of the clove tree, and red spider mites. These insects, however, are disturbed by the presence of the ant, and *Ctenarytaina* sp., abundant at certain times of the year, was seldom observed on clove trees occupied by *O. longinoda*. Similarly, in the nursery, red spider damage to clove seedlings was sometimes serious, but was noticed only once on seedlings colonised by the ant.

Small colonies of two small ant species, namely *Cardiocondyla wroughtoni* (For.) var. *bimaculata* Wh. and *Tapinoma melancephalum* (F.) were found nesting in cracks in the trunk and fruits of coconut palms occupied by *O. longinoda* but they probably occupy a part of the tree not foraged by *O. longinoda*.

Complete collections of the various insects caught by *O. longinoda* were not made, but during observations in the course of other experiments, insects in the process of being killed by the ant were recorded. These included fourteen species of Hemiptera Heteroptera, twenty-eight species of Hymenoptera, thirty-eight species of Coleoptera and twenty-six other insect and Arthropod species. They included last-instar nymphs of the large Coreid, *Anoplocnemis curvipes* (F.), nymphs of *Theraptus* (Way, 1951) and an adult of *Helopeltis bergrothi* Reut., a pest of cacao in Zanzibar. The Hymenoptera included honey bees, wasps, and workers of ant species, particularly driver ants (DORYLINAE) and the large Ponerine ant, *Paltothyreus tarsatus* (F.), isolated individuals of which are commonly observed foraging on the ground. The Coleoptera included CARABIDAE, the Curculionid, *Diaecoderus conspersus* (Gerst.), adults of which attack foliage of the clove tree, and some large CETONIIDAE. Limbs and wings of the last-named as well as of grasshoppers and large cockroaches were severed by the ants and the various parts of the body carried separately to the nests. Web-spinning spiders were common in trees occupied by *O. longinoda* and, while on their webs, were not molested but, when shaken off, even the largest species were attacked and sometimes killed.

The efficiency of predation by *O. longinoda* is shown by the scarcity of other insects (apart from Homoptera) in coconut palms inhabited by this ant, by comparison with the rich insect population in palms occupied by the generally less aggressive ants, *Anoplolepis longipes* and *Pheidole punctulata* (Way, 1953*b*). It is remarkable that certain small birds were found building nests and successfully rearing broods in trees occupied by *O. longinoda*, often close to the ant nests (Pl. VII, fig. 4). This was observed so frequently that it can only be explained on the basis of selection by the birds of such a nesting site which undoubtedly affords protection from some of their natural enemies.

The method by which *O. longinoda* attacks the honey bee, *Apis mellifera* L. and the ant, *Dorylus* (*Anomma*) *nigricans* Illiger was observed. *A. mellifera* were attracted to dishes of honey placed in the nursery for *O. longinoda* colonies. Some bees were deterred by the aggressive attitude of the ants but many eventually settled on the dish and were immediately attacked. A single ant was often able to hold down a bee for several seconds until others came to its assistance. They gripped the wings, limbs, antennae and mouth-parts with their mandibles and spreadeagled the insect, holding it in this position for up to twenty minutes. The soft cuticle of the limb and abdominal joints was sometimes pierced by the mandibles of the ants which occasionally curved their abdomens over their backs and ejected poison on to the wound. The bee was eventually killed or paralysed and was then carried to the nest by several workers. This process was also observed in coconut palms where bees visit the large inflorescences. Here the ants seldom deterred the bees and on one occasion five bees were observed being killed or carried to the ant nests from a single inflorescence.

O. longinoda workers were often seen killing workers of driver ants (DORYLINAE). On one occasion a 2-inch wide stream of *Dorylus nigricans* was crossing the ground between two trees occupied by *O. longinoda*. Many large workers of *O. longinoda* clustered on both sides of the stream and seized any *D. nigricans* workers that strayed from the main stream. The *D. nigricans* soldiers were neither attacked nor did they defend their workers. *O. longinoda* workers carried the dead or paralysed *D. nigricans* workers to their nests and, over a period of one hour, three hundred and forty-eight were taken to one tree, and two hundred and fifty-two to the other.

O. longinoda workers defend their colonies against many interfering animals. Giant arboreal millipedes were usually attacked, but appeared to be undamaged. The aggressive attitude of the ant towards human beings depends on distance from the nest. Worker ants on the trunks of trees and on the ground rarely responded aggressively to interference but, on the clusters of Homoptera which they were attending, and particularly near the nests, they attacked furiously, biting painfully and ejecting " poison ". The poison does not seem to increase the pain caused by the bite, nor does the pain persist after removal of the ant; it seems to be used mainly for defence, because it was seldom observed to be used during predation but was frequently ejected in response to interference and in defence against the ant *Pheidole punctulata*.

Discussion.

Nixon (1951) has suggested that, if ants are used to combat insect pests, the predominantly carnivorous species should be preferred, because their association with Homoptera is too loose for the latter to benefit from it. No such species appear to have been used successfully. In fact, it is doubtful whether they could be used for biological control, because the highly organised ant community requires a dependable source of food, and, even with the wealth of insect life in the tropics, the large colonies of the carnivorous DORYLINAE are nomadic because the supply of insect food in any one area is insufficient to maintain static colonies. Thus DORYLINAE, which were estimated by Vosseler (1905) to have once collected about 1,600,000 insects from a single field in ten days, have only a temporary influence on the insect population in any one area. Moreover, they are mainly ground foragers and appear to have little effect on insects living in trees. Other primarily carnivorous ants, such as the PONERINAE, form small, insignificant colonies and have little influence on insect populations in general. Many have become specialised in their choice of prey; for example *Paltothyreus tarsatus* which feeds almost entirely on termites.

There is no doubt that the most successful ant species, and thus the ones most easily used for biological control, are those which have a dependable source for a proportion of their food. As a result they are able to maintain successful static colonies. Of these, the ants *Oecophylla smaragdina* and *O. longinoda* are of undoubted value as beneficial predators.

Fears have been expressed that the Homoptera, tended by *O. longinoda*, might themselves become pests and the following observations bear on this problem :—

O. longinoda usually attends Stictococcids and Coccids which so far have not been incriminated as vectors of plant viruses and apparently it does not attend Aphids and Pseudococcids (which may be virus vectors) except under conditions where the former insects do not thrive or are not available.

The level of population of those Coccids which depend on attendance by *O. longinoda*, and consequently the extent of mechanical damage that they cause to plants, is directly related to the population level of the attendant ant colony (Way, 1954). There is no doubt that a comparatively small *O. longinoda* population can provide effective biological control but, in Zanzibar, the population is often excessive. Thus, the worker population of *O. longinoda* on a 15 to 20 ft. clove tree is commonly in the region of fifty to one hundred thousand, whereas a population of less than ten thousand workers suffices to protect a coconut palm completely against attack by the Coreid, *Theraptus* sp. In one coconut plantation badly infested by *Theraptus*, 2,920 workers of *O. longinoda* were counted in nests on a large undamaged palm. Probably no more than 5,000 worker ants were present on the tree.

In Zanzibar, the economic damage caused by Homoptera attended by *O. longinoda* appeared to be most serious on small trees and shrubs. For example, the young stems and leaves of coffee (*Coffea excelsa* and *C. liberica*) sometimes supported large populations of Coccids and attendant *O. longinoda* and the bushes seemed in poor condition by comparison with uncolonised ones. On cacao, dense populations of *O. longinoda* were not observed, but the Homoptera were sometimes concentrated on the developing fruits, which consequently suffered damage, although the plants themselves appeared healthy. (On large trees such as the coconut palm and the mango, damage caused by the Homoptera was not noticeable. With the coconut palm this was partly because it appears unable to support such high ant populations as can many other trees and shrubs.)

It has already been emphasised (Ghesquière, 1939) that the introduction of *Oecophylla* species for use as beneficial predators should not be considered before carrying out careful experiments on the possible damage that might result from their associated Homoptera. In this respect, it is of interest to refer again to the practice adopted in southern China (Friederichs, 1920; Groff & Howard, 1925). Here, in certain areas, the winter is too severe for *O. smaragdina* to survive, and nests of the ants are introduced from warm regions each year in early summer. The ants protect the *Citrus* crop during the summer and die on the approach of winter. Probably, during this time, the ant colonies, and hence the Homoptera, cannot increase greatly even if reproductive forms of the ant are present and therefore the damage caused by the Homoptera is probably insignificant.

Where protection is required throughout the year, it is necessary to maintain permanent colonies of *Oecophylla* spp. together with the harmful Homoptera which they attend. Under these conditions, it is questionable whether *O. longinoda* can be used on such crops as coffee and cacao, but on the coconut palm there is no doubt that the damage caused is insignificant compared with the benefits derived from protection against *Theraptus*. This is almost certainly true of the essentially similar problem in the Solomon Islands where *O. smaragdina* is a predator on *Amblypelta cocophaga* (Phillips, 1940).

In connection with insect pests of the coconut palm, the probable economic advantages of using *Oecophylla* spp. to control *Theraptus* and *Amblypelta cocophaga* make it necessary to consider the following factors which affect successful establishment of colonies in coconut plantations. Counts made in Zanzibar showed that when more than 70 per cent. of the palms were colonised 142 42
by *O. longinoda*, damage by *Theraptus* to uncolonised palms was slight.

The chief difficulty in establishing such colonies is that certain other species of ant attack *Oecophylla*, and have eliminated it from large areas in East Africa and in the Solomon Islands. In addition, other difficulties which would be encountered include the antagonism between ants from different colonies, and the fact that a fertilised queen must, apparently, be present in introduced colonies.

One observation of some importance in relation to both the successful establishment and the maintenance of colonies in coconut palms is that when these were interplanted with other trees preferred by the ants, such as clove and *Citrus*, the queen was invariably on the latter. Furthermore, dense populations of the ant in coconut plantations were found only where the palms were interplanted with clove, *Anacardium occidentale*, *Bridelia micrantha*, *Canthium zanzibaricum* and *Citrus* spp. In such plantations the ants were not confined to the preferred plant but colonised the coconut palms as well.

The probable benefits derived by *Oecophylla* spp. from interplanting include :—

(1) The resulting dense populations are more successful in deterring other non-beneficial ant species. (2) Larger numbers of sexual forms will be produced

giving an increased chance of establishing further colonies. (3) The favoured host plants will be more suitable than the coconut palm for initiation of a colony by a young queen. (4) With a range of host plants there is a wider range of choice of Homoptera, and thus a more dependable source of honey-dew.

In addition, the question of canopy is important. Although *O. longinoda* workers move across the ground, the extension of colonies is favoured by closed canopy foliage or, in its absence, by some other inter-connection. For example, in Mafia Island, poles of a local tree, used to support telephone wires, had sprouted and had been colonised, for a length of over two hundred yards, by one *O. longinoda* colony, the wires providing the runways. In southern China (Groff & Howard, 1925), *Citrus* growers provide artificial runways of bamboo to facilitate the spread of *O. smaragdina* between trees, and in the Solomon Islands O'Connor (1950) has suggested that fallen fronds could be used for this purpose.

Summary.

In British East Africa *Oecophylla longinoda* (Latr.) var. *textor* Santschi is locally common in the coastal region. Inland it is absent from higher altitudes and from areas where there is a pronounced dry season.

In Zanzibar Island, *O. longinoda* colonises at least 89 species of trees and shrubs; the largest populations occur on the clove (*Jambosa caryophyllus*), *Citrus* spp., *Bridelia micrantha* and *Canthium zanzibaricum*.

The nesting habits and colony composition of *O. longinoda* are such that one colony may spread over a number of adjacent trees; it contains only one gravid queen.

Winged virgin sexual forms are released at the beginning of the wet seasons and new colonies are initiated by a single queen, who uses her food reserves to bring the first batch of brood to maturity.

In Zanzibar, *O. longinoda* tends a wide range of Homoptera that produce honey-dew, but apparently " prefers " certain Coccids, notably *Saissetia* spp.

The degree of attention afforded by an ant species determines the species of Homoptera which it is able to attend.

The insect species preyed upon by *O. longinoda* include the honey bee, *Apis mellifera*, and the driver ant, *Dorylus nigricans*, of which large numbers may be destroyed.

O. longinoda is of undoubted value for controlling certain coconut pests, notably *Theraptus* sp. (Coreidae), and its efficiency in coconut plantations could probably be much enhanced.

Acknowledgements.

I am greatly indebted to Dr. F. J. Nutman, O.B.E., for his encouragement and valuable criticisms, and also to Dr. W. J. Hall, C.M.G., for valuable advice and for the trouble he took in identifying many species of Homoptera. Grateful acknowledgement is due to Dr. D. J. Williams who also identified many species of Homoptera and to Mrs. J. James who did much of the botanical work. I also wish to thank Mr. Said Himid for assistance with the field studies and Mr. J. Townsend for drawing the text figures.

References.

* Bondar, G. (1922). As lendas e a verdade sobre a formiga caçarema da Bahia e seu papel na lavoura.—Chacaras e Quint., **26**, pp. 369–371. (R.A.E., (A) **11**, p. 90.)

* Bünzli, G. H. (1935). Untersuchungen über coccidophile Ameisen aus den Kaffeefeldern von Surinam.—Mitt. schweiz. ent. Ges., **16**, pp. 453–593. (R.A.E., (A) **23**, p. 679.)

---

* Original not examined.

Carpenter, G. D. H. (1920). A naturalist on Lake Victoria.—London, Fisher Unwin.

Corbett, G. H. (1937). Division of Entomology. Annual Report for 1936.—Gen. Ser. Dep. Agric. S.S. & F.M.S., no. 26, pp. 29–48.

Dodd, F. P. (1902). Notes on the Queensland green tree ants (*Oecophylla smaragdina*).—Vict. Nat., Melb., **18**, pp. 136–142.

Doflein, F. (1905). Beobachtungen an den Weberameisen (*Oecophylla smaragdina*).—Biol. Cbl., **25**, pp. 497–507.

Friederichs, K. (1920). Weberameisen und Pflanzenschutz.—Tropenflanzer, **23**, pp. 142–150.

Garcia, C. E. (1935). A field study on the Citrus Green Bug, *Rhynchocoris serratus* Donovan.—Phillipp. J. Agric., **6**, pp. 311–325.

Garcia, C. E. (1939). The Citrus Rind Borer and its control.—Phillipp. J. Agric., **10**, pp. 89–92.

* Groff, G. W. & Howard, C. W. (1925). The cultured citrus ant of South China.—Lingnaam agric. Rev., **2**, pp. 108–114. (R.A.E., (A) **13**, p. 227.)

Ghesquière, J. (1939). Un capside myrmécoïde nuisible au caféier.—Rev. Zool. Bot. afr., **33**, pp. 30–32.

Hingston, R. W. G. (1927). The habits of *Oecophylla smaragdina*.—Proc. ent. Soc. Lond., **2**, pp. 90–94.

* de Jong, J. K. (1934). *Helopeltis* in cacaotuinen.—Bergcultures, **8**, pp. 658–667. (R.A.E., (A) **23**, p. 402.)

Leefmans, S. (1934). Ziekten en plagen der cultuurgewassen in Nederlandsch Oost-Indië in 1931.—Meded. Inst. PlZiekt., Buitenz., no. 82, 92 pp.

Matheson, J. K. & Bovill, E. W. (1950). East African Agriculture.—London, Oxford Univ. Pr.

Murray, G. H. (1937). Outbreak *Promecotheca antiqua*—Lindenhafen Estate.—New Guinea agric. Gaz., **3**, no. 2, pp. 1–2.

Nixon, G. E. J. (1951). The association of ants with Aphids and Coccids.—36 pp. London, Commonw. Inst. Ent.

Nutman, F. J. & Sheffield, F. M. L. (1949). Studies of the clove tree. I. Sudden-death disease and its epidemiology.—Ann. appl. Biol., **36**, pp. 419–439.

O'Connor, B. A. (1950). Premature nutfall of coconuts in the British Solomon Islands Protectorate.—Agric. J. Fiji, **21**, pp. 21–42.

Phillips, J. S. (1940). Immature nutfall of coconuts in the Solomon Islands.—Bull. ent. Res., **31**, pp. 295–316.

* Pickel, B. (1927). Ainda existe quem queira comprar cuyabanas?—Chacaras e Quint., **36**, pp. 184–185. (R.A.E., (A) **15**, p. 610.)

* Prell, H. (1925). Ameisen als Schutz gegen Raupenfrass.—Forstl. Wschr. Silva, **1925**, no. 7, repr. 16 pp. (R.A.E., (A) **13**, p. 208.)

* Ridley, —. (1890). (On *Oecophylla*.)—J. Straits Br. Asiat. Soc., **1890**, p. 345. (Cited by Wheeler, W. M. (1910). Ants, their structure, development and behaviour, p. 628, New York, Columbia Univ. Pr.)

Simmonds, H. W. (1924). Mission to New Guinea, Bismarcks, Solomons and New Hebrides.—Coun. Pap. Fiji, **1924** no. 2, 13 pp.

---

* Original not examined.

STRICKLAND, A. H. (1947). Coccids attacking cacao (*Theobroma cacao*, L.) in West Africa, with descriptions of five new species.—Bull. ent. Res., **38,** pp. 497–523.

STRICKLAND, A. H. (1951). The entomology of swollen shoot of cacao. II. The bionomics and ecology of the species involved.—Bull. ent. Res., **42,** pp. 65–103.

TRYON, H. (1919). Report of the Entomologist and Vegetable Pathologist.—Rep. Dep. Agric. Qd, 1918–19, pp. 37–49.

VAN HALL, C. J. J. (1922). Ziekten en plagen der cultuurgewassen in Nederlandsch-Indië in 1921.—Meded. Inst. PlZiekt., Buitenz., no. 53, 46 pp.

VOSSELER, J. (1905). Die Ostafrikanische Treiberameise (Siafu).—Pflanzer, **1,** pp. 289–302.

* VOÛTE, A. D. (1935). *Cryptorrhynchus gravis* F. und die Ursachen seiner Massenvermehrung in Java.—Arch. néerl. Zool., **2,** pp. 112–142. (R.A.E., (A) **24,** p. 198.)

WAY, M. J. (1951). An insect pest of coconuts and its relationship to certain ant species.—Nature, Lond., **168,** p. 302.

WAY, M. J. (1953*a*). Studies on *Theraptus* sp. (Coreidae); the cause of the gumming disease of coconuts in East Africa.—Bull. ent. Res., **44,** pp. 657–667.

WAY, M. J. (1953*b*). The relationship between certain ant species with particular reference to biological control of the Coreid, *Theraptus* sp.—Bull. ent. Res., **44,** pp. 669–691.

WAY, M. J. (1954). Studies on the association of the ant *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae).—Bull. ent. Res., **45,** pp. 113–134.

WHEELER, W. M. (1922). Ants of the Belgian Congo.—Bull. Amer. Mus. nat. Hist., **45,** pp. 224–231.

WIGG, L. G. T. (1936). Report of the Silviculturist.—Rep. Dep. Agric. Zanzibar, 1935, pp. 34–41.

WILLIAMS, D. J. (1953). On a new species of *Saissetia* (Hem. : Coccoidea) from Zanzibar.—Bull. ent. Res., **44,** pp. 581–582.

---

* Original not examined.

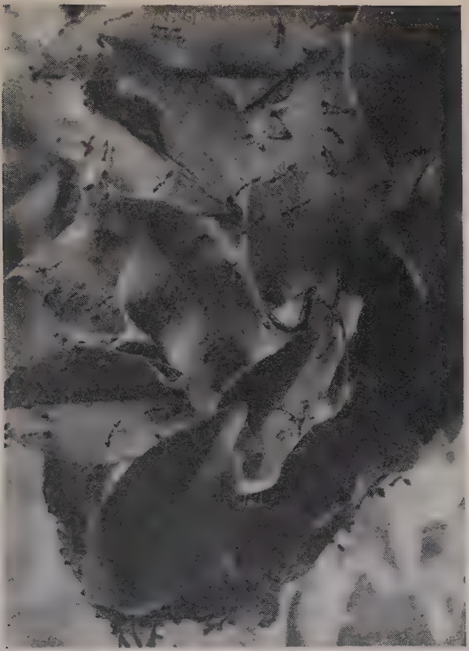


Fig. 1. Part of *O. longinoda* nest on the clove tree (*Jambosa caryophyllus*). The leaves have been drawn together with a thick web of silk threads.

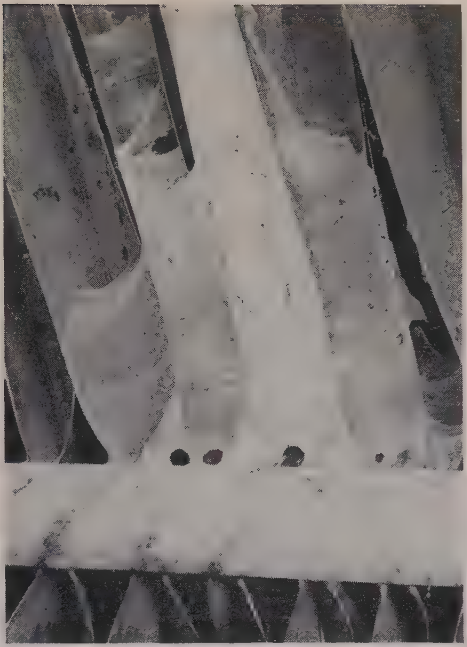


Fig. 2. Part of a small nest of *O. longinoda* on the coconut palm. A silk web has been built across the undersides of several leaflets which are Λ shaped in transverse section.

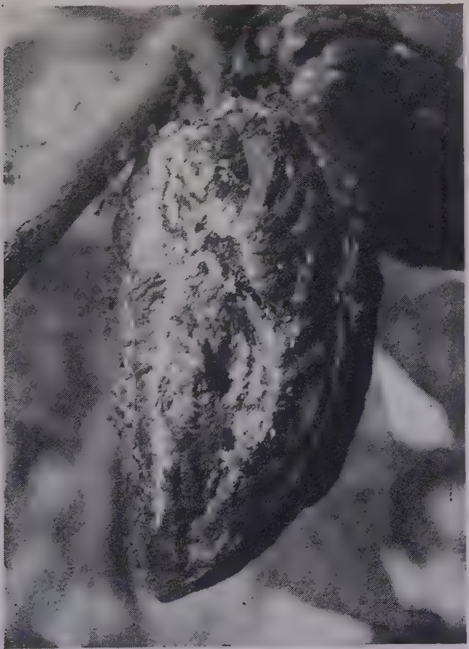


Fig. 3. Developing fruit of cacao, (*Theobroma cacao*) infested with clusters of *Pseudococcus* sp. attended by *O. longinoda*. The former have caused necrotic lesions on the fruit.

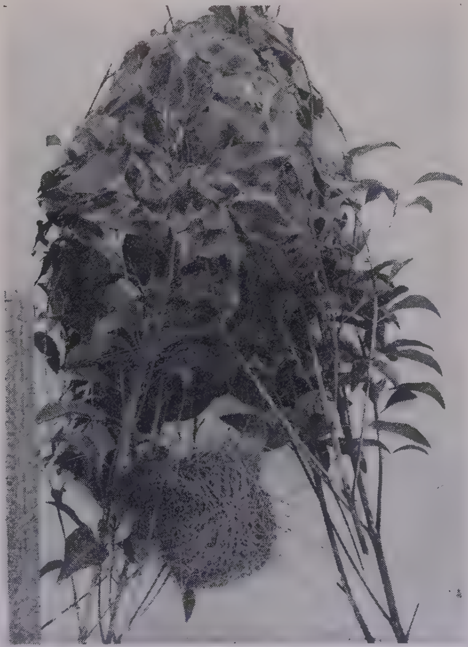


Fig. 4. Bird's nest which was built and used to rear brood successfully beneath a large nest of *O. longinoda* on the clove tree.

STUDIES ON THE ASSOCIATION OF THE ANT *OECOPHYLLA LONGINODA* (LATR.) (FORMICIDAE) WITH THE SCALE INSECT *SAISSETIA ZANZIBARENSIS* WILLIAMS (COCCIDAE).

By M. J. Way.
*Clove Research Scheme, Zanzibar.**

(Plate VIII.)

Some species of Homoptera attended by ants cause severe mechanical damage to plants and others are vectors of plant virus diseases (Carter, 1933; Serrano, 1934; Strickland, 1947). It is generally assumed that the ants increase the damage caused to the plants because they benefit the Homoptera, notably by transporting and disseminating them and also by protecting them from various enemies. Nixon, however, has pointed out (1951) that few ant species have been shown to transport Homoptera (Lubbock, 1882; Dutt, 1912; Hough, 1922; Bunzli, 1934), and that, although they may accidentally protect them from parasites and predators (Herzig, 1937), the efficiency of protection has often been exaggerated.

The work described here originated from studies on the sudden-death disease of clove trees which was once thought to be caused by a virus, *Saissetia zanzibarensis* Williams (Coccidae) being suspected as a vector (Nutman & Sheffield, 1949). This Coccid is abundant on the clove tree in association with the ant *Oecophylla longinoda* (Latr.), but it was not found in the absence of the ant. Consequently it was thought that, if *O. longinoda* were destroyed, *S. zanzibarensis* would be eliminated and virus transmission stopped.

Field experiments to determine the effect on *S. zanzibarensis* of destroying the attendant *O. longinoda* were followed by work on the nature of the association between the two insects.

Experimental.

Work on the biology of *O. longinoda* and on the various Homoptera with which it is associated is published elsewhere (Way, 1954). Briefly, *O. longinoda* is a tree-nesting species, which, in Zanzibar, has been found colonising over eighty-nine species of trees and shrubs, and attending many different species of Homoptera that produce honey-dew. Leaves are bound together to make nests and the Homoptera are found, inside and outside the nests, on leaves, stems and inflorescences.

The clove tree (*Jambosa caryophyllus*) is a favoured nesting site for *O. longinoda*; the ant attends six species of Coccidae found on it, of which *Saissetia zanzibarensis* is easily the most common. The male *S. zanzibarensis* has not been observed but, if similar ~~to~~ that of other Coccids, it would be short lived, and unable to secrete honey-dew; thus it is of no significance to the ants. The present work was done on the parthenogenetic female, which passes through two nymphal instars before moulting to the adult. All stages, except possibly the young first instar, produce honey-dew, nymphal instars producing relatively little compared with the adult. The nymphs, and to a less extent the young adults, can crawl but, before reproducing, the adults develop a sclerotised cuticle and become sedentary.

---

* Seconded from Rothamsted Experimental Station, Harpenden.

S. zanzibarensis, attended by *O. longinoda*, has been found on thirty species of trees and shrubs (Way, 1954). It is most abundant on the clove tree where it aggregates on the pedicels and buds of developing inflorescences, and also on stems up to about one year old, both inside and outside the *O. longinoda* nests. It is not common on two- to three-year-old branches, and only occurs on leaves when crowded within the nests. It was not found on the larger branches and trunks of mature trees.

Effect of the Removal of the Attendant *O. longinoda.*

Experiment 1.

All nests of *O. longinoda* were removed from two clove trees, approximately 15 ft. high, containing thriving colonies of the ant and scale. Most of the remaining ants were destroyed by treating the main branches with 0·05 per cent. γ BHC in a wettable powder, the few survivors being destroyed by hand. Over one hundred twigs each bearing clusters of 20–200 *S. zanzibarensis* were left on the trees. Neighbouring trees, all of which bore thriving ant-scale colonies, were used as controls.

Three days after removing the ants, it was noticed that a few young nymphal scales had migrated from the original clusters and had settled down on hitherto uncolonised twigs. Those remaining had produced copious honey-dew, with which most were contaminated. Weekly examinations showed a decrease in the number of Coccids until, after three weeks, only a few nymphs could be found and many dead adults with parasite emergence holes were observed. After a month, only fifteen living *S. zanzibarensis* could be found on one tree, and none on the other. Throughout this period thriving clusters of the scale persisted in the neighbouring trees colonised by *O. longinoda.*

The same fall in Coccid population occurred in a similar experiment using *Saissetia nigra* (Nietn.) tended by *O. longinoda* on *Bridelia micrantha.*

Experiment 2.

On two clove trees colonised by *O. longinoda* and *S. zanzibarensis*, six branches bearing clusters of the scale were isolated from the ant colonies by means of grease-bands and all ants on them destroyed by hand. Another six branches, left in contact with the ant colonies were used as the control. Table I shows the total numbers of *S. zanzibarensis* present on treated and control branches at the beginning of the experiment and after four weeks. The figures are not strictly accurate, owing to the difficulty of counting the young nymphs in crowded clusters.

TABLE I.

Total numbers of *S. zanzibarensis* present in branches of clove trees before and after exclusion of the attendant *O. longinoda* by grease-banding, compared with numbers present in branches from which *O. longinoda* was not excluded.

Treatment	Total number of *S. zanzibarensis* per treatment	
	At the beginning	After four weeks
O. longinoda present ..	3120	2280
O. longinoda absent ..	2820	162

Experiment 3.

Eight clusters of *S. zanzibarensis* on twigs of a clove tree colonised by *O. longinoda* were each enclosed in an organdie-covered cage (Pl. VIII, fig. 1). The ants were removed from four cages and the twigs bearing the Coccids completely enclosed within the organdie. The remaining four cages were left open at the base to allow the ants free access. Table II shows the total numbers of scales at the beginning of the experiment, and also after two and four weeks.

TABLE II.

Total numbers of *S. zanzibarensis* present on clove twigs before exclusion of the attendant *O. longinoda* compared with numbers present on twigs from which *O. longinoda* was not excluded.

Treatment	Total number of *S. zanzibarensis* per treatment		
	At beginning	After two weeks	After four weeks
O. longinoda present . .	172	192	276
O. longinoda absent . .	188	52	48

The above experiments show that there was rapid and considerable reduction in the population of *S. zanzibarensis* after removal of the *O. longinoda.* Also, the scale was found only once on a clove tree not colonised by *O. longinoda*, when it occurred as a cluster of about thirty individuals attended by the ant *Crematogaster castanea* F.Sm. on a tree recently vacated by *O. longinoda.*

The dependence of *S. zanzibarensis* on *O. longinoda* was so striking that further studies were made, mainly under nursery conditions, to determine the nature of the benefits derived by the two insects from the association.

Methods.

The experiments were done under the partial shade of a roof of mangrove poles, giving conditions not dissimilar to those in the field. The plants used were potted clove seedlings, which, unless otherwise stated, were 1 to 2 years old and 1 to 2 feet in height. The *S. zanzibarensis* were established by laying infested clove twigs from the field on the seedlings to which the nymphs migrated as the twigs died. The scales generally clustered on the lower part of the main stem of each seedling.

The tree-nesting habit of *O. longinoda* proved useful for experimental establishment of colonies. Ten to twenty potted seedlings bearing *S. zanzibarensis* were placed on a 3 ft. × 2 ft. 6 in. table with 6 in. legs, resting in dishes of oil (fig. 1). This not only prevented the *O. longinoda* from escaping but also prevented other ant species, notably *Pheidole punctulata* Mayr, from invading the colony.

Lamp glasses were inverted over one or more clove seedlings, to form artificial nests; each was enclosed in white cloth to exclude radiant heat from the sun. *O. longinoda* nests were collected from the field, and the ants lightly anaesthetised with carbon dioxide. Brood and adults were usually separated, the brood being placed in the artificial nests, and the workers on the table. Within a few hours the workers were assiduously attending the brood, and soliciting the *S. zanzibarensis* for honey-dew. Within a week they had usually begun to build new nests, to which the brood was eventually carried. Care was taken to ensure that the introduced brood contained young and medium sized larvae which produce the silk required for nest building. It was possible to establish colonies more easily by introducing cut branches bearing nests of *O. longinoda*; as the branches died the ants moved to the potted seedlings on which they built new nests. A disadvantage of this technique was that there were many *S. zanzibarensis* in the introduced nests, and there was a risk that some would migrate or be transferred to the seedlings, thus affecting the counts of scale population.

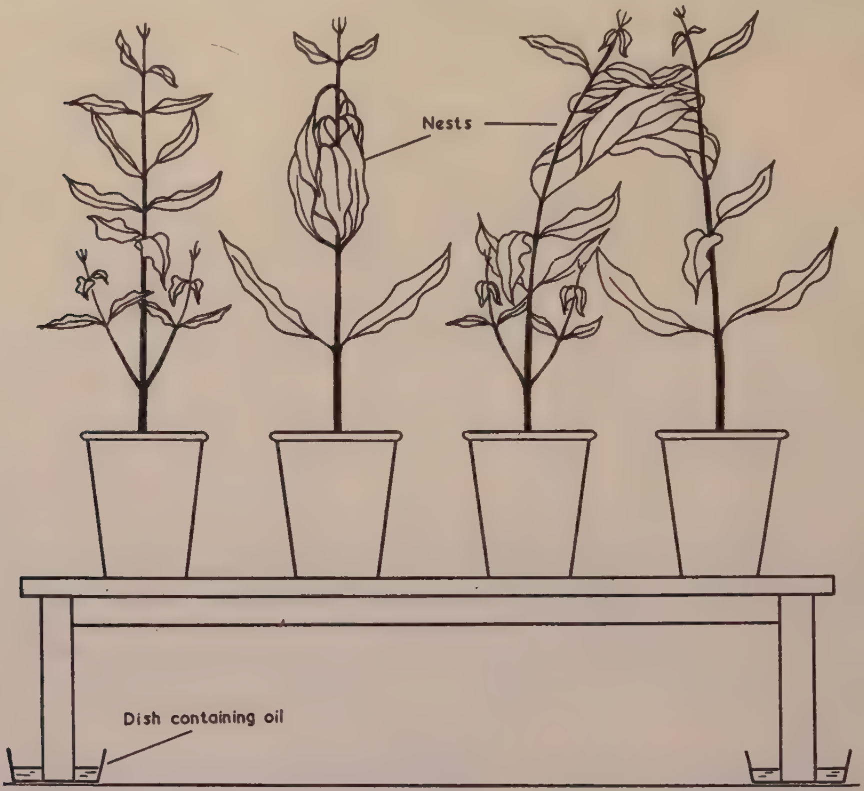


Fig. 1.—Side view of small table and four clove seedlings used for maintaining colonies of *O. longinoda* and *S. zanzibarensis* in the nursery. Leaves of the seedlings were drawn together by the ants to form nests. Clusters of *S. zanzibarensis* attended by the ants were present in the younger growth of the clove stems.

If the ant colony contained no queen, brood collected in the field was introduced from time to time. This presented no difficulty for, although there is antagonism between adult workers from different colonies, there is none towards the immature forms.

Fig. 2 shows the methods used for enclosing *O. longinoda* with *S. zanzibarensis* on single clove seedlings. In some experiments clove seedlings in 7-in. pots ringed with a 1–2-in. wide grease-band were infested with *S. zanzibarensis* (fig. 2, *a*). Adult workers or workers and brood of *O. longinoda* were then deposited on the surface of the soil in the pots. If suitable brood was present the ants built small nests by binding together several leaves. When known numbers of workers were required the ants were lightly anaesthetised with carbon dioxide and, after determining the volume occupied by a known number, the required batches were measured out in a 2-in. × 1-in. specimen tube.

When it was necessary to exclude parasites and predators of *S. zanzibarensis*, a cylindrical metal frame, 1 ft. 6in. high by 6 in. diameter, covered with thin parachute nylon was placed over each seedling and the base pressed firmly into the soil (fig. 2, *b*). The ants were introduced through a sleeve at the top of the cage. A celluloid roof was sometimes fitted to exclude rain (fig. 2, *c*.).

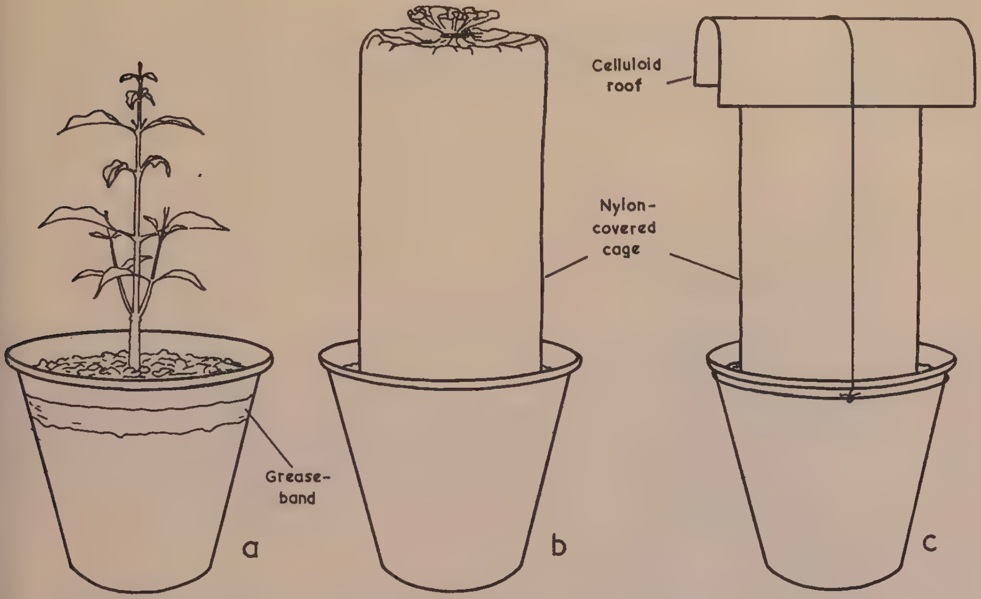


Fig. 2.—Methods used for enclosing *O. longinoda* and *S. zanzibarensis* on single clove seedlings. *a*, seedling uncaged to allow access of parasites of *S. zanzibarensis*; *b*, seedling caged to prevent access of parasites of *S. zanzibarensis*; *c*, caged seedling covered with "roof" to prevent entry of rain.

Effect of Removal of Honey-Dew by *O. longinoda*.

Contamination by excess honey-dew is potentially most serious among the gregarious species of Homoptera. Of these, certain Aphidae, such as *A. fabae* Scop., do not become severely contaminated and the gregarious habit is probably of value in concentrating them at the best feeding sites (Ibbotson & Kennedy, 1951). *S. zanzibarensis*, however, is strongly gregarious, and forms very dense clusters; it becomes severely contaminated except when it is attended by *O. longinoda* which solicits the Coccid with its antennae and imbibes the honey-dew which is excreted in response.*

There seems to be no quantitative evidence to support the general opinion that contamination by honey-dew is deleterious to Homoptera and that ants, by removing it, are benefiting them. This was studied in nursery experiments.

Fifteen potted clove seedlings, infested with first-instar nymphs of *S. zanzibarensis*, were caged individually (fig. 2, *c*). Batches of five plants were treated as follows:—

(a) *O. longinoda* absent. Rainfall being excluded, the removal of contaminating honey-dew by this means was prevented.

---

* In the field, during periods of heavy rainfall, *O. longinoda* workers were sometimes unable to remain in attendance on *S. zanzibarensis*. When this occurred the excreted honey-dew was washed on to the surrounding leaves and a growth of sooty moulds developed in it.

(b) *O. longinoda* absent. Aerial parts of plants washed with rainwater twice daily using a watering can with a fine rose. This did not prevent contamination, but much of the excreted honey-dew was removed.

(c) As in (b) but a large population of *O. longinoda* maintained in each cage. Contamination by honey-dew did not occur. The watering was not necessary for removal of honey-dew, but was done to standardise conditions in treatments (b) and (c).

In each treatment, counts of total numbers of *S. zanzibarensis* were made at intervals for 132 days, the results being shown graphically in fig. 3.

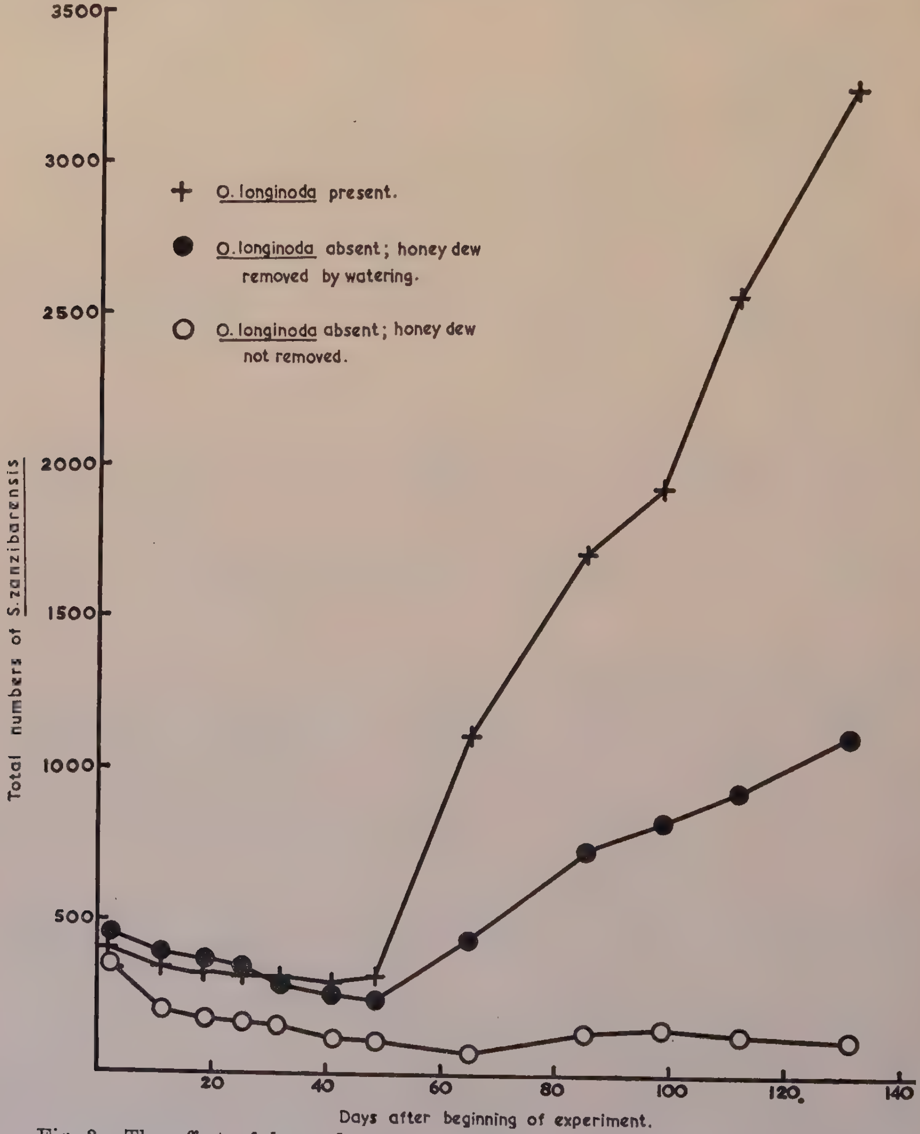


Fig. 3.—The effect of honey-dew contamination on development of populations of *S. zanzibarensis*. In the presence of the attendant *O. longinoda* contamination was entirely prevented, while watering the aerial parts of the seedlings reduced the severity of contamination.

It can be seen that in treatment (a) (no ants, no watering), the total number of Coccids fell from 388 to a relatively low level of 100–150. During the first 20 days a film of honey-dew appeared on most of the nymphal scales and contamination increased as they reached maturity at 30 to 50 days. Large drops of honey-dew could be seen hanging from some of the adult Coccids (fig. 4, *a*), on which a growth of sooty mould (*Meliola* sp. PERONOSPORACEAE) developed, eventually covering them and the surrounding parts of the plant (fig. 4, *b*). These Coccids soon died, presumably of asphyxiation. Most of the young nymphs, produced after about 60 days, were apparently asphyxiated by the honey-dew; some died during ecdysis. A few, however, became established and the total population remained at over 100 individuals, despite severe honey-dew and sooty mould contamination.

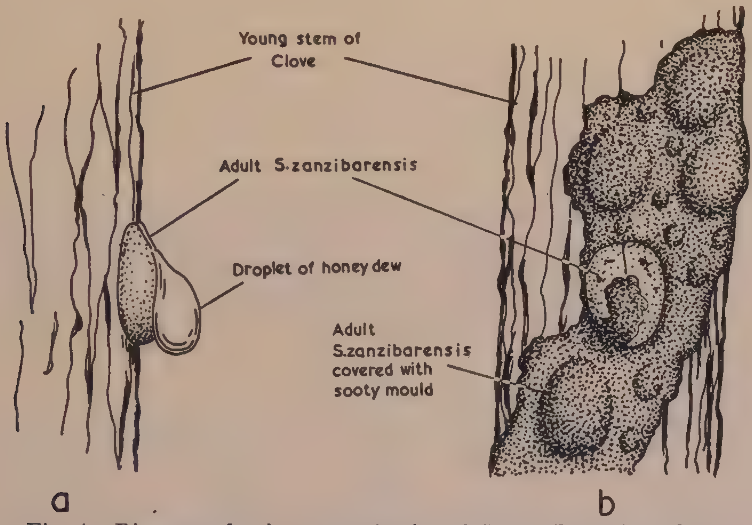


Fig. 4.—Diagrams showing contamination of *S. zanzibarensis* by honey-dew and sooty mould. *a*.—Droplet of excreted honey-dew hanging from an adult *S. zanzibarensis*. *b*.—Adults and nymphs of *S. zanzibarensis* covered by a sooty mould (*Meliola* sp.) which is growing on the excreted honey-dew.

In treatment (b) (no ants, watered) some loss of nymphs and young adults occurred during the first 40 to 50 days, after which reproduction started and the population increased to 1,080 after 132 days. Honey-dew contamination occurred during the periods between each watering and sooty mould developed after about 60 days but it was relatively slight compared with treatment (a). Clearly, the washing reduced contamination and benefited the scale, probably in two ways, first by reducing nymphal mortality, and secondly by increasing longevity and fecundity of the adult.

In treatment (c) (ants present, watered), there was at first a slight fall in scale population but then reproduction started and the population rose rapidly to about 3,220 after 132 days (fig. 3). Honey-dew and sooty mould contamination did not occur.

The large increase in population in the treatment where ants were present, compared with that in which honey-dew contamination was partly avoided by watering, requires explanation. Undoubtedly honey-dew was removed more efficiently by the ants, but it seems that they may confer additional benefits. For example, *O. longinoda* workers have been observed freeing scales, and the surrounding parts of the plant from contaminating moulds; they also remove dead scales from which parasites have emerged. During the wet seasons, scales contaminated by honey-dew sometimes developed a growth of *Trichoderma* sp. (Fungi Imperfecti). This fungus, apparently a parasite, caused the curtailment of some experiments, but was never observed attacking *S. zanzibarensis* in the presence of *O. longinoda* or during the dry seasons.

General Attention by *O. longinoda.*

Besides removing honey-dew and fungal contaminations, there are, as already mentioned, other possible benefits which *O. longinoda* may confer on *S. zanzibarensis* and the effect of these should be most marked when the ant population

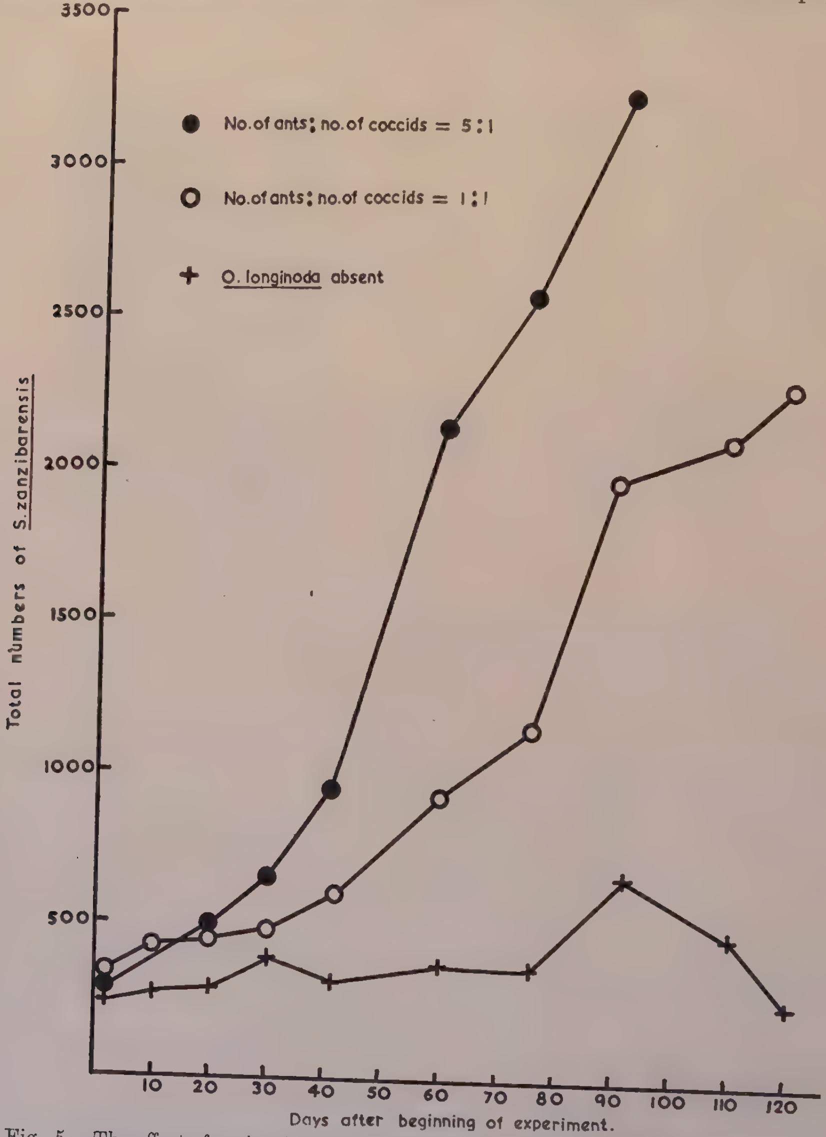


Fig. 5.—The effect of maintaining the numbers of *O. longinoda* and *S. zanzibarensis* at different ratios on the rate of increase of *S. zanzibarensis* populations.

is high relative to that of the scale. In an experiment to test this, three batches of five potted clove seedlings infested with 300–400 *S. zanzibarensis* per batch were caged as in fig. 2,*b*. The treatments were:—

(a) *O. longinoda* present. No. of ants: no. of scales = about 5 : 1.

(b) *O. longinoda* present. No. of ants: no. of scales = about 1 : 1.

(c) *O. longinoda* absent. Aerial parts of each plant watered twice daily, as in previous experiment, to reduce honey-dew contamination.

During the experiment the ratio of ants to scales was maintained by introducing the required ant workers or brood after each count of the Coccid population. To do this, those originally in the cages were removed and replaced by a fresh batch, thus ensuring that antagonistic worker ants from different colonies were not mixed. At first only adult workers were used but towards the end of the experiment, when conditions became overcrowded, young larvae were also used.

Fig. 5 shows graphically the total numbers of *S. zanzibarensis* in each treatment at intervals during the period of the experiment.

In treatment (a) (ant-scale ratio 5 : 1) the scale population increased, in 91 days, to 3,250, about tenfold. At this stage two clove seedlings died, possibly from feeding damage by the large number of scales. In treatment (b) (ant-scale ratio 1 : 1) the scale population also rose, though not so rapidly, to 1,995. Where there were no ants, the scale population remained low (the fall in numbers after 91 days was probably due to the presence of *Trichoderma* sp.). Contamination by honey-dew did not occur in either of the treatments containing the ant. This shows that all available honey-dew was consumed; thus the scale population, even in treatment (b) (ant-scale ratio 1 : 1) excreted insufficient honey-dew for the ants. The marked excitability and aggressiveness of the ants in treatment (a) (ant-scale ratio 5 : 1) may be a symptom of acute starvation. This experiment was repeated with similar results and it is clear that, honey-dew removal being equally effective in treatments (a) and (b), there must be other benefits conferred by the ant to explain the large difference in the rates of increase of *S. zanzibarensis* population.

Transport and Dissemination of *S. zanzibarensis*.

Under experimental conditions, young twigs of small clove trees infested with *S. zanzibarensis* and caged with large populations of *O. longinoda* showed an increase in numbers of scale until the twigs died from feeding damage. Such damage was not observed in the field.

Five clove trees colonised by *O. longinoda* and *S. zanzibarensis* were examined at intervals for a year. It was found that, except within nests, a cluster of *S. zanzibarensis* seldom comprised more than 400 individuals; also, no cluster remained on the same twig for longer than five months. A seasonal variation in position of clusters on the tree was observed and is illustrated in fig. 6. It seems that the number of scales in a cluster is limited as is the length of time it remains on a particular twig. The effect of the ant on movement of the scales was studied.

Four seedlings colonised by *O. longinoda* and *S. zanzibarensis*, were placed on a small table (fig. 1). Six uncolonised seedlings were introduced, of which four were connected by 6-in.-long wooden " bridges " to the colonised seedlings. In the centre of each " bridge " was a 1/5 in. wide gap, which was insufficient to interfere with the passage of ant workers, and each pot was grease-banded to prevent passage of ants from seedling to seedling by any means except by the bridges. Thus, the ants could not colonise the two seedlings which were not connected to the others. Further, the grease bands and the 1/5 in. gap in each " bridge " prevented access of crawling scales to any of the six uncolonised seedlings. After three days, many young nymphs with a few older nymphs and young adults of *S. zanzibarensis* were found on one formerly uncolonised plant and workers of *O. longinoda* were seen carrying single nymphs across a bridge to it. Each nymph was placed in position and solicited for a few seconds by the ant. By the following day the ant workers had transferred nymphs to a second bridged plant, and eventually all four bridged plants were colonised. Those which were isolated remained free from scales until the end of the experiment four months later.

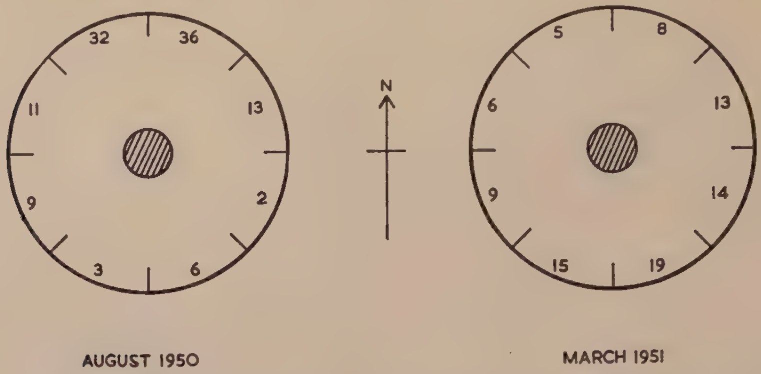


Fig. 6.—Diagrammatic plan of the crown of a clove tree colonised by *O. longinoda* and *S. zanzibarensis* showing the seasonal variation in position of *S. zanzibarensis* clusters. Figures are given for the numbers of twigs bearing *S. zanzibarensis* clusters in different sectors of the tree crown.

In another experiment, a clove seedling colonised by *O. longinoda* and *S. zanzibarensis* was connected to an uncolonised seedling by a 16-ft. bridge of telephone wire with a 1/5 in. gap as before. After eleven days a nest had been built in the originally uncolonised seedling, and the workers were seen transferring nymphal scales to it by way of the bridge.

These observations show that *O. longinoda* transports and establishes *S. zanzibarensis*. In this connection an important field observation by Nutman should be recorded. Nutman (priv. comm.) observed an ant colony deserting a dying clove tree. A stream of worker ants, some carrying apparently living individuals of *S. zanzibarensis*, was seen moving to another tree several hundred yards away. Nests and scales were eventually established on the second tree.

It seems that *O. longinoda* workers select the feeding sites for *S. zanzibarensis*. When the latter were established experimentally on clove seedlings in the absence of the ant, the great majority clustered on the lower, older part of the stem. *O. longinoda* on the other hand always established them on the younger growth of the upper part of the stem, although with continued reproduction the clusters eventually spread to the lower parts of the seedling. Both sites seem equally suitable. To summarise: *O. longinoda* workers transport the *S. zanzibarensis*, establish them at suitable feeding sites, and maintain the number of individuals in a cluster at a level which does not cause obvious injury to the twigs of the host plant.

Influence of Parasites on Scale Populations.

Twigs bearing *S. zanzibarensis*, collected from clove trees colonised by *O. longinoda*, were placed in parasite emergence boxes, and several Hymenopterous parasites of the Coccid were obtained, indicating that the ant does not confer absolute protection to the scale from parasitism.

Two parasite species belonging to the genus *Coccophagus* (APHELINIDAE) were recognised. Of these, one, an undescribed species, was rare by comparison with the other, which is similar to *C. nigritus* Comp. The former will be referred to as *Coccophagus* sp. nov., and the latter as *Coccophagus* sp. nr. *nigritus*. Parasitised *S. zanzibarensis* could not be recognised by superficial examination until after pupation of the parasite. The pupal *Coccophagus* sp. nr. *nigritus* become pigmented before emergence and at this stage can be distinguished through the transparent dorsal cuticle of the still living nymphal *S. zanzibarensis*. As far as is known this species, in contrast to the other, is not parasitic on the adult scale.

The pupa of *Coccophagus* sp. nov. within the young adult scale, which is killed by the parasite either at pupation or during the pupal period, could be recognised by the dull brown colour and brittle appearance of the unsclerotised dorsal cuticle of the host. When pupation of *Coccophagus* sp. nov. occurred after the cuticle of the adult host had become sclerotised and opaque, parasitism was recognised only by the exit hole of the adult parasite.

Clusters of *S. zanzibarensis* collected in the field, from inside and outside nests of *O. longinoda*, were examined as described above for pupae of *Coccophagus* sp. nr. *nigritus*.

Table III shows that scale clusters on twigs outside the *O. longinoda* nests were parasitised by *Coccophagus* sp. nr. *nigritus* despite attendance by the ant. Other observations showed that parasitism may also be severe (parasite pupae observed in up to 14 per cent. of scales) even when such scale clusters are covered by silken shelters (see Pl. VIII, figs. 3–5). It seems, however, that, within the ants' nests, *S. zanzibarensis* is rarely attacked by the parasite (Table III).

TABLE III.

Examination of *S. zanzibarensis* in *O. longinoda* colonies for pupae of the parasite *Coccophagus* sp. nr. *nigritus*.

Position of *S. zanzibarensis* clusters	*O. longinoda* colony	No. of nests or twigs	Total no. *S. zanzibarensis* (except 1st-instar nymphs)	% *S. zanzibarensis* containing parasite pupae
Outside *O. longinoda* nest	a	9	327	17
	b	11	781	5
Within *O. longinoda* nest	a	3	563	0·4
	b	2	482	0

O. longinoda workers did not react to the presence of adult *Coccophagus* sp. nr. *nigritus*, but the latter always moved out of the way when an ant approached and consequently were continually being disturbed in their search for suitable hosts or during oviposition. *Coccophagus* sp. nr. *nigritus* were seen ovipositing in second-instar nymphs of *S. zanzibarensis*. The parasite crawled on to a nymph and usually inserted its ovipositor towards the posterior end of the scale, the process taking 10–20 seconds. This would explain its inefficiency as a parasite within the nests of *O. longinoda*, where disturbance would be frequent.

The behaviour of *Coccophagus* sp. nov. in the presence of *O. longinoda* was not studied, but oviposition in the adult *S. zanzibarensis* was observed to take over one minute; this probably explains its relative inefficiency as a parasite of *S. zanzibarensis* when attendant *O. longinoda* workers are present.*

The influence of parasites, in the absence of ants, on populations of *S. zanzibarensis* was studied as follows:—Four treatments were set up, each of six clove seedlings infested with *S. zanzibarensis*, in pots. The scales were established some weeks previously and were maintained, until required, in a colony of *O. longinoda.* Thus some reproducing adult scales were present from the beginning of the experiment. The treatments were:—

(a) Pots grease-banded, and uncaged, with *O. longinoda* excluded.

(b) As (a) but with large population of *O. longinoda.*

(c) Seedlings caged to exclude parasites (fig. 2,*b*). *O. longinoda* excluded.

(d) As (c) but with large population of *O. lcnginoda.*

Treatments (a) and (b) were shaded with a canopy of nylon to give conditions similar to treatments (c) and (d). In all treatments the clove seedlings were watered twice daily to reduce honey-dew contamination as far as possible and thus allow the separate effects of insect parasites to be studied. Watering was unnecessary in the *O. longinoda* treatments but was done to standardise environmental conditions throughout all treatments.

Parasitism was rare in the nursery, so a source was provided. Twigs bearing parasitised *S. zanzibarensis* were collected in the field from a clove tree whose ant population had been destroyed ten days previously; these were placed among the plants in treatments (a) and (b). Fig. 7 shows graphically the numbers of scales in each treatment at intervals during 90 days. The counts of observable *Coccophagus* spp. pupae in the treatments exposed to parasitism are also given.

As in all previous experiments, the attendant *O. longinoda* caused a marked rise in scale populations, although in the uncaged treatment there was an initial fall. This occurred in two experiments and its significance is not known. Where the ants were absent there was a marked difference between the caged and the uncaged treatments. In the former, the scale population rose slightly and remained at just above its original level of 437, while in the uncaged treatment it fell sharply from 523 until only one nymphal Coccid was alive after 90 days. In this treatment, after about 20 days (fig. 7), many scales contained pupae of the two *Coccophagus* species, but the extent of parasitism does not appear sufficient to account for the marked initial fall. However, it should again be emphasised that only those parasites which were in the late pupal stage at the time of examination were counted; also some parasites passed through the pupal stage and emerged as adults during the intervals between each count and thus only a proportion of the total *Coccophagus* spp. population was recorded. Whether or not parasitism was responsible for the initial fall in treatment (a), there is no doubt that *Coccophagus* spp. were responsible for the eventual reduction of the scale population to a single individual. In two other experiments a reduction of the scale population to zero was recorded after 69 and 110 days, whereas the population in parasite-free treatments, although remaining relatively low in the absence of *O. longinoda* never approached zero.

To summarise:— In the absence of *O. longinoda*, the population of *S. zanzibarensis* remains at a low level, providing parasites are excluded; if *Coccophagus* spp. are present the scale is virtually exterminated.

---

* By contrast, *Eulecanium* sp., sometimes tended by *O. longinoda* on the clove tree, is parasitised by a *Cecidomyiid* (subfamily CECIDOMYIINAE, tribe CECIDOMYIARIAE, subtribe TRIFOLA), and even inside the ants' nests up to 30 per cent. of the Coccids bore medium and large larvae of the ectoparasite. A careful examination for eggs and small larvae was not made, and thus the total parasitism was probably higher. Presumably the ovipositor of the ectoparasite is not inserted through the cuticle of the host; hence oviposition may be accomplished quickly and is not prevented by ant disturbance.

As can be seen in fig. 7, few *S. zanzibarensis* were parasitised by *Coccophagus* spp. when *O. longinoda* was present; the observation that the adult parasites are not attacked by the ant suggests that protection is accidental. (*Cf.* Herzig, 1937.) In this connection it was noticed that clusters of *S. zanzibarensis* and other Homoptera tended by *O. longinoda* on leaves and developing nuts of the coconut palm, were sometimes associated with large numbers of the Diaspidids *Aspidiotus destructor* Sign., *Hemiberlesia lataniae* (Sign.) and *Phenacaspis inday* (Banks), which were uncommon elsewhere. It seemed that the Diaspidids which do not produce honey-dew and are not solicited by the ant, were incidentally protected by it from their natural enemies. (*Cf.* Flanders, 1945.)

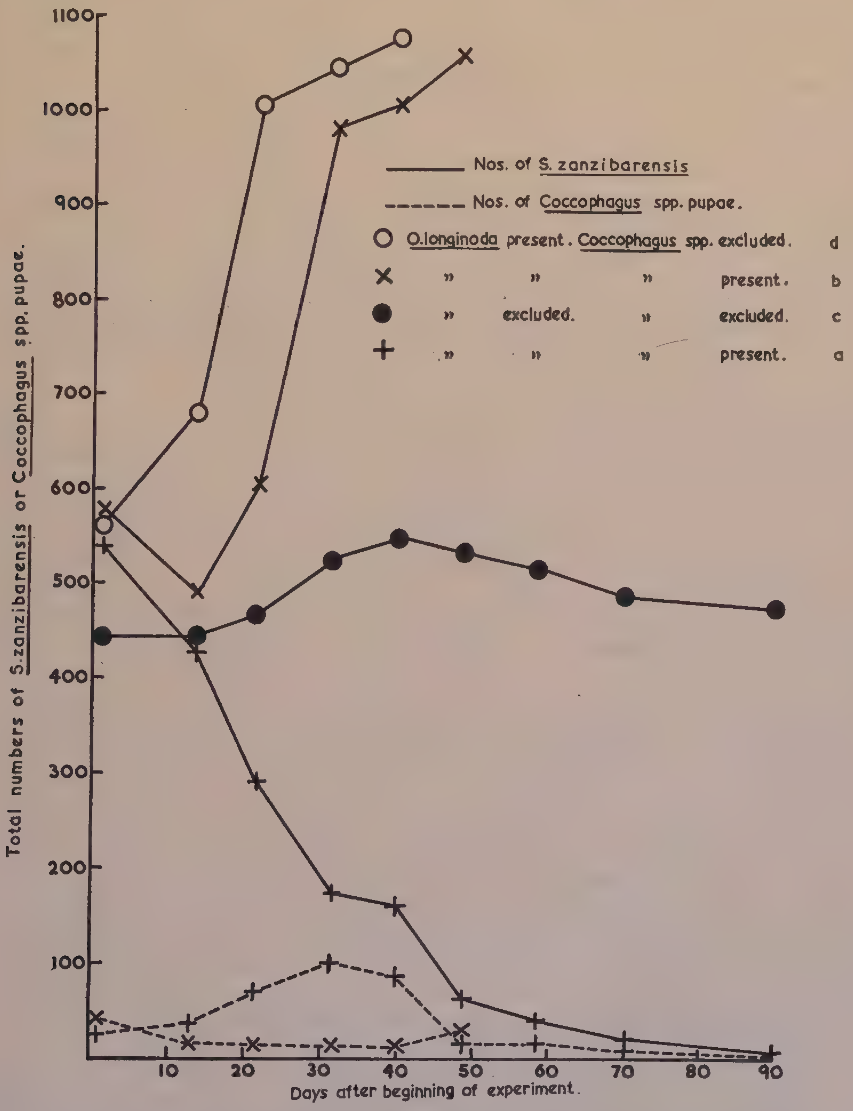


Fig. 7.—The effect of parasitism by *Coccophagus* spp. on populations of *S. zanzibarensis* in the presence and in the absence of the attendant *O. longinoda*.

Effect of Predators on Populations of *S. zanzibarensis*.

Lepidoptera.

The larvae of certain Lepidoptera are well known predators of Coccids in the tropics, and Jacobson (1913) has described the behaviour of two species of *Eublemma* (Noctuidae) which, as larvae, are predatory on Coccids tended by the ant *Oecophylla smaragdina* (F.). In colonies of *O. longinoda*, several larvae of a species of *Eublemma*, predatory on *S. zanzibarensis*, were found. These often occurred within nests of the ant, each being covered with a tough silken structure which in some species was encrusted with portions of cuticle of the scales which had been consumed (Pl. VIII, fig. 2). Such larvae were not interfered with by the ant and they pupated within the nests. Presumably the emerging adults are able to escape from the nests without being molested. The following species were identified:—*Eublemma costimacula* (Saalm.); *E. pyrochroa* Hmps.; *E. scitula* (Ramb.). None of these species was sufficiently abundant to cause noticeable reduction of *S. zanzibarensis* populations.

Coleoptera: Coccinellidae.

No Coccinellids were found attacking *S. zanzibarensis* or other Homoptera tended by *O. longinoda*. This is due to predation by the ant which drives away or kills all free-living Coleoptera in trees that it occupies (Way, 1953, 1954). Coccinellids occur elsewhere and two species, *Chilocorus wahlbergi* Muls. and *Exochomus* sp., were found attacking *S. zanzibarensis* on clove seedlings placed in an area where *O. longinoda* was absent. Thus *O. longinoda*, because it is a predator, completely protects *S. zanzibarensis* from attack by Coccinellids. No other insect predators of *S. zanzibarensis* were found.

Significance of Shelters Built by *O. longinoda* over Clusters of *S. zanzibarensis*.

Reference has already been made to the silken shelters that *O. longinoda* may build around clusters of *S. zanzibarensis* and other Homoptera which it tends. The meshwork enclosing a young flowering shoot of clove is shown in Plate VIII, fig. 3, and in Plate VIII, fig. 4, a fruit of rambutan (*Nephelium lappaceum*), both bearing *S. zanzibarensis*. On the latter the silk meshwork has been attached to the spines which project from the fruit. On vegetative twigs of the clove, 3–4 leaves may be bound together with silk, or the shelter may consist of silk alone; sheets of silk mesh several inches square are built over clusters of *S. zanzibarensis* and other Coccids on coconut fruits. (Pl. VIII, figs. 5 & 6).

The silk meshwork is generally closely woven, thus preventing the passage of small insect parasites, and yet it does not protect *S. zanzibarensis* from the parasite *Coccophagus* sp. nr. *nigritus* which must use the same entrances as the ant workers.

Most shelters are built in the wet seasons, and during heavy rain in November 1951 it was noticed that the worker ants remained within the shelters soliciting *S. zanzibarensis* for honey-dew whereas they retreated from exposed scale clusters. The shelters were not waterproof but they protected the ants from battering by the rain and prevented dislodged individuals from falling to the ground. In the wet seasons (approx. March–May and Nov.–Dec.) there are prolonged periods of rainfall during which the silken shelters must be of importance in enabling the ants to continue collecting the honey-dew.

Dependence of *O. longinoda* on *S. zanzibarensis*.

The foregoing evidence has shown that *S. zanzibarensis* is markedly dependent on the presence of the attendant *O. longinoda*. It would be of interest to determine whether the ant is also dependent on the scale.

The main sources of food for *O. longinoda* are honey-dew from certain Homoptera, and other insects on which the ant is predatory (Way, 1954). Insects attacked are limited to those on the surface of soil and vegetation because the ant only forages in exposed situations. Dead insects and nectar are minor sources of food.

The following shows the relative importance of the two main sources of food:—

(a) A single *O. longinoda* colony, covering about 1/5 acre, may consist of at least half a million individuals. Within the limits of the colony the population of available insects for predation is generally extremely low (Way, 1954), and it seems that the large static colonies could not be maintained on the insufficient and unreliable insect diet.

(b) Thriving colonies of *O. longinoda* are found on mangroves, particularly *Sonneratia caseolaris* which often occur in tidal waters. *O. longinoda* workers have not been seen foraging on the mangrove swamp at low tide, and thus must obtain their food from the Homoptera which they tend and from the relatively few other insects that they catch on the mangrove trees.

(c) In a clove plantation, six small trees colonised by *O. longinoda* and *S. zanzibarensis* were grease-banded to prevent the ant workers from foraging on the ground. Eight months later the colonies on two trees were thriving. On the other four there were few ants, but this was due to the absence of queens and consequent cessation of reproduction in these trees (see Way, 1954).

(d) A thriving colony of *O. longinoda* with *S. zanzibarensis* was maintained in the nursery (fig. 1) for 14 months. There was no queen, and therefore ant brood was added occasionally to maintain the numbers. It is possible that some of the brood was eaten by the ants, but otherwise the honey-dew-producing scales were the sole source of food for the worker ants and for the developing brood.

The above evidence shows that *O. longinoda* colonies can thrive when practically the only food is that supplied by the Homoptera which they attend. Other sources of food are insufficient and unreliable and thus it seems that there is marked interdependence in the association between the ant and the scale. One aspect of this, the relationship between numbers of *O. longinoda* and of *S. zanzibarensis* was studied experimentally.

Relationship Between Relative Numbers of *O. longinoda* and *S. zanzibarensis*.

Twenty clove seedlings, of which nine were infested with *S. zanzibarensis*, were placed on each of three small tables (fig. 1). The scales were established several weeks previously and, therefore, some reproducing adults were present at the beginning of the experiment. Ants were added to each batch of seedlings as follows:—

Treatment	(a)	approximately	500	*O. longinoda* workers
,,	(b)	,,	5,000	,, ,,
,,	(c)	,,	10,000	,, ,,

O. longinoda larvae were added at intervals during the experiment to maintain the worker population approximately constant at the original levels. It should be emphasised that conditions in this experiment differed from those in an experiment previously described in which the ant/Coccid ratio was maintained at fixed levels throughout the experiment.

Fig. 8 shows the total number of *S. zanzibarensis* in each treatment at intervals for 125 days.

In the treatment where the worker ant population was maintained at about 500, the scale population fell from 932 to 456 within the first sixteen days. From the beginning, the great majority of workers solicited the scales normally but during the first three days a few of the larger workers (four on one occasion) attacked them. A worker inserted its mandibles into a scale and remained in this position for about a minute. If the victim was a nymph, it was then torn from the plant. Mature adult scales were usually too firmly attached to be

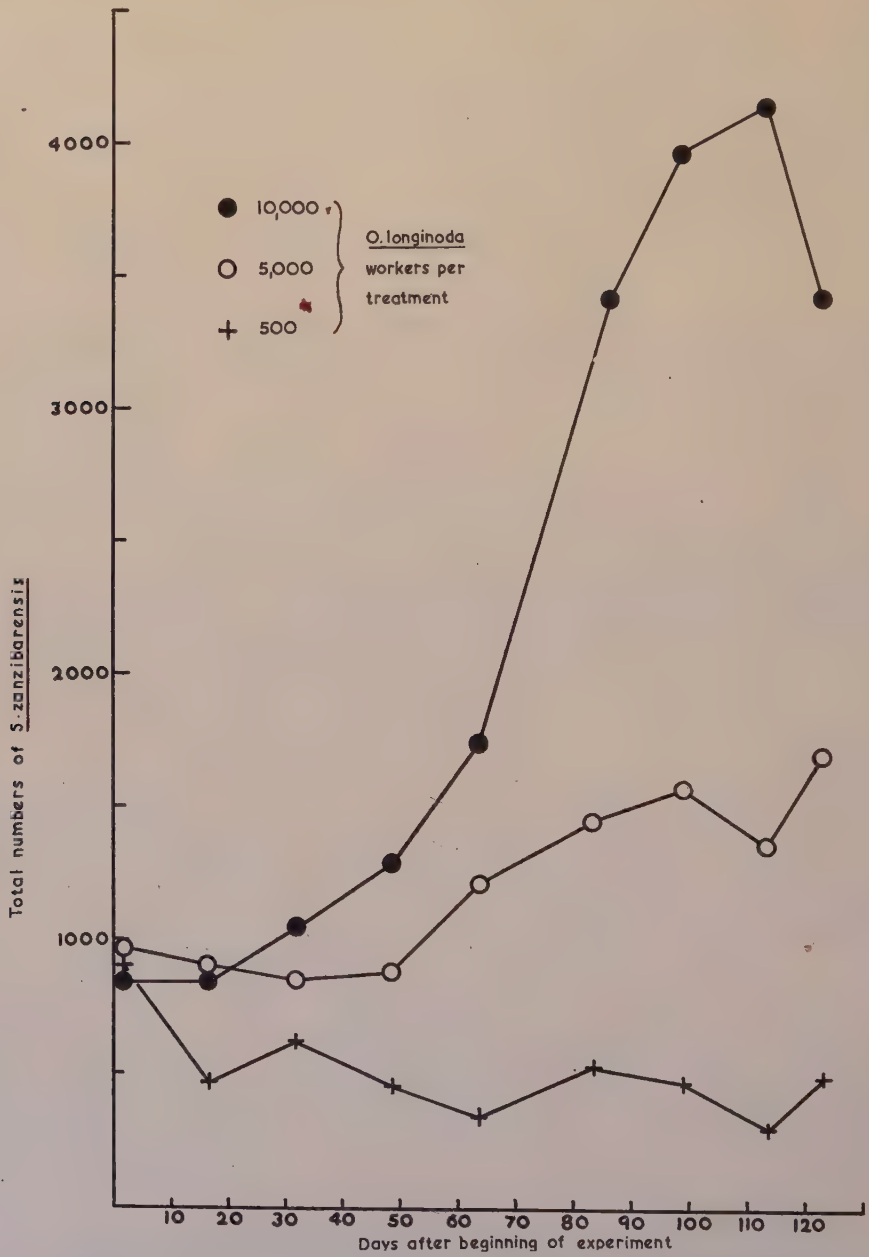


Fig. 8.—The effect of the level of ant population on the numbers of *S. zanzibarensis* maintained within an *O. longinoda* colony.

removed in this way, and were destroyed piecemeal until all that remained attached to the plant was a peripheral rim of cuticle. Some of the scales were carried to the edge of the table and dropped over. Others were removed to the nest, apparently for food, though there was no obvious selection of particular individuals for this purpose. The destruction ceased after six days, when presumably the scale population had been reduced to a level which just satisfied the honey-dew requirements of the ant population. As a consequence, honey-dew was not produced in excess and contamination of the scales did not occur. The first count of the *S. zanzibarensis* population was made after 16 days, and from then until the end of the experiment at 125 days the numbers fluctuated between 295 and 615. Once during this period a worker was observed attacking a scale, and it is probable that destruction occurred whenever the scale population began to rise above the level which satisfied the honey-dew requirements of the ant colony. Mature scales produce more honey-dew than do the immature forms, and thus their age distribution determines the number of scales required by a particular number of ants.

Destruction of *S. zanzibarensis* by *O. longinoda* workers occurred in another experiment when a dish of honey was provided for a five-months-old colony in the nursery. Many of the ant workers collected the honey and ceased to solicit the scales, while a few began to destroy large numbers of them. When all the scales on three of the nine clove seedlings had been destroyed, the dish of honey was removed; on the following day destruction had ceased. After ten days, nymphs had been re-established by the ants on two seedlings and after about two months all three seedlings bore thriving clusters of *S. zanzibarensis*. In both experiments, it was noticeable that destruction of excess scales occurred mainly on the seedlings that were furthest from the ants' nests.

In the present experiment (fig. 8) the treatments containing worker ant populations of about 5,000 and 10,000 showed increases in scale populations until after about 100 days, when the numbers began to fluctuate, suggesting that the required populations had been reached. It is noteworthy that, as before, the rate of increase was more rapid in the treatment where food-shortage of the ants was most marked. The experiment was not continued for a sufficient period to show the exact levels of *S. zanzibarensis* populations maintained by ant populations of 5,000 and 10,000 workers. However, as shown in Table IV, the figures obtained during the last 40 days of the experiment are striking.

TABLE IV.

The levels of *S. zanzibarensis* populations reached in colonies containing different numbers of *O. longinoda* workers.

Approx. no. of ant workers	Initial no. of *S. zanzibarensis*	Mean no. of *S. zanzibarensis* during last 40 days	Ratio no. ants : no. Coccids during last 40 days
500	932	447	1 : 0·9
5,000	983	1440	1 : 0·3
10,000	823	3760	1 : 0·4

Thus the level of the *S. zanzibarensis* population in an *O. longinoda* colony depends on the number of ants, and scales in excess are killed or, if insufficient are present, their numbers increase to a level which satisfies the food requirements of the ant colony.

Discussion.

This work has shown that in the association between the ant, *O. longinoda*, and the Coccid, *S. zanzibarensis*, the latter depends on the ant and is rare in its absence. The ant is also dependent on the scale which is its major source of food, other sources being unreliable and probably incapable of maintaining more than a relatively low population.

Although the closeness of the association between ants and Homoptera may vary according to the species concerned it seems that, even when there is notable interdependence, some of the advantages derived by each insect from the association are incidental (Nixon, 1951). Thus, protection of the Homoptera from parasites and sometimes predators is due to accidental disturbance by the ants, and not because they are recognised as such. Similarly, ants engaged in collecting honey-dew for food are only incidentally beneficial to the Homoptera. The present work has shown that *O. longinoda* does not react to parasites of *S. zanzibarensis*. Also towards Coccinellid predators, the response is the same as that evoked by any insect on which it is normally predatory, whether near *S. zanzibarensis* clusters or elsewhere. *O. longinoda* workers, however, show certain modifications of behaviour which apparently enable them to profit from their association with *S. zanzibarensis*, namely:—

(1) The habit of stroking the scale insect with the antennae which induces excretion of honey-dew. This solicitation is shown by most ant species which are associated with honey-dew-producing Homoptera and though sometimes it may appear aimless (Smith, 1942) there is no doubt that it is evoked by the presence of the Homoptera.

(2) The habit of enclosing *S. zanzibarensis* clusters in silken shelters, a process in which several worker ants co-operate, some of them carrying the larvae which secrete the silk. The shelters do not give added protection to the Coccid from parasites (*Coccophagus* spp.) but they protect the ant during adverse weather, enabling it to continue collection of honey-dew. Strickland (1951) considers that shelters built by Crematogasterine ants over *Pseudococcus* spp., though not protecting them from parasites, protect them from Coccinellid predators. *Oecophylla* shelters, however, are not needed for protection against Coccinellids. *Pheidole* spp. not only build shelters over the Homoptera which they attend, but also covered runways of similar construction from their nests to the shelters. This suggests that shelters built by *Oecophylla*, like *Pheidole* runways, primarily protect the ant, and may be only incidentally beneficial to the Homoptera.

(3) The habit of transporting the Coccid to suitable feeding sites. This seems to be the most significant evidence of the intimate association between *O. longinoda* and *S. zanzibarensis*. Many ant species do not transport the Homoptera which they tend, but there are a few exceptions, notably *Lasius* spp. (Lubbock, 1882), which collect and guard Aphid eggs in winter and, in spring, place the hatching Aphids on young shoots of the food plant.

Special mention should be made of the relationship between the level of ant and Homoptera populations. The latter may flourish when attended by ants and some, attended by *Pheidole* spp. (Kirkpatrick, 1927; Carter, 1933), *Iridomyrmex humilis* (Mayr) (Woglum, 1919; Barber, 1923; Wheeler, 1927), and Crematogasterine species (Strickland, 1951), are more numerous in their presence than in their absence. This was very noticeable in the present work which has also shown that, within the *O. longinoda* colony, a ratio is maintained between the ant population and that of *S. zanzibarensis*. A similar relationship probably exists between other ant species and the Homoptera which they tend, providing the latter benefit from the association. As shown by Smith and Armitage (1951) *Iridomyrmex humilis* is assiduous in its attentions to honey-dew-producing

Homoptera when its food supply is scarce and, under these conditions, efficiently protects them from parasites and predators. It might be inferred that when the numbers of Homoptera rise to a level that provides honey-dew in excess of the ants' requirements, the latter will tend to neglect them and consequently they would then suffer from honey-dew-contamination and from parasite and predator attack, according to the degree of neglect. In this way a balance would be maintained between the numbers of Homoptera and attendant ants.

The present work has shown that the *S. zanzibarensis* population is controlled not in this way, but by the destruction of excess Coccids by *O. longinoda* workers. Such excess Coccids may be carried to the nest, and are perhaps used for food as are other insects on which the ant is normally predatory. This aspect of behaviour has not been observed previously. Nixon (1951), in discussing observations by Negi, Misra and Gupta (1930), and Strickland (1947), has suggested that ants may feed on active nymphal Coccids, but not on adults which have become sedentary, and have begun to secrete honey-dew freely. *O. longinoda*, however, has been observed killing both sedentary adult and active nymphal *S. zanzibarensis* but only when they were present in excess. Establishment of newly hatched nymphs, and consequent build-up of scale population, was most rapid when the ants were living under starvation conditions; thus starvation does not induce the ant to destroy them for food.

The normal attitude of the *O. longinoda* worker towards *S. zanzibarensis* is not aggressive. Its movements are relatively slow and deliberate, in many ways resembling its behaviour towards its brood. In contrast, an entirely different and aggressive pattern of behaviour is shown by the worker ant while destroying excess scales. It is not possible to reconcile these observations with the theory advanced by Herzig (1937), who suggested that certain ants (*Lasius* spp.) are both repelled and attracted by Aphids, repelled because the Aphids are themselves unpalatable, but attracted because they are a source of honey-dew. This theory implies that when the ants do not require honey-dew they are repelled by the Aphids which consequently are not attacked. This does not apply to the behaviour of *O. longinoda* towards *S. zanzibarensis*.

The aggressive response of *O. longinoda* workers to *S. zanzibarensis* is characterised by rapid and jerking movements of the limbs with the mandibles open and abdomen upraised. Its attitude during attack on the Coccid is the same as that adopted towards insects on which it is normally predatory. This suggests that *O. longinoda* is attracted to *S. zanzibarensis* because the latter is a source of honey-dew, but also can be antagonistic because the scale, like many other insect species, incites aggression and is itself a source of food. Apparently, the attitude of the ant depends on the degree to which its desire for honey-dew, which initiates one behaviour pattern, overcomes its predatory instinct which initiates the other behaviour pattern.

It should be noted that the aggressive and predatory behaviour of *Oecophylla* species is exceptional for an ant that is associated with honey-dew-producing Homoptera. Thus, species of *Pheidole* and *Iridomyrmex* are normally considered to be aggressive (Perkins, 1913; Wheeler, 1934), but the effects of their predation are less marked than those of *Oecophylla* spp. (Phillips, 1940; Way, 1953, 1954). It seems probable that, when it is not actuated by the need for honey-dew, the behaviour of an ant species towards the source of honey-dew is consistent with its normal attitude to other insects. Thus, the behaviour of *O. longinoda* is conditioned by its aggressive predatory attitude. Other relatively non-aggressive ant species may show no response, while relatively timid species (*e.g.*, certain *Lasius* spp.) in which the predatory instinct is poorly developed, and which depend almost entirely on honey-dew for food, would perhaps be repelled by the Homoptera (APHIDAE) when they are not being attracted to them by their need for honey-dew.

Summary.

A close association exists between the ant *Oecophylla longinoda* (Latr.) and the scale insect *Saissetia zanzibarensis* Williams.

Several factors cause the scale to be rare in the absence of the ant. Contamination by honey-dew and sooty moulds prevents increase of the *S. zanzibarensis* population above a relatively low level, while, in addition, insect parasites and probably predators virtually exterminate the scale. A fungal parasite may destroy honey-dew-contaminated *S. zanzibarensis* under humid conditions.

The attendant *O. longinoda* prevents contamination of the scale by honey-dew. It gives absolute protection from Coccinellid predators and, although parasitism by *Coccophagus* spp. and predation by *Eublemma* spp. is not prevented, the mortality of *S. zanzibarensis* which they cause is thought to be of little significance.

O. longinoda workers benefit *S. zanzibarensis* in other ways. They remove débris from the scale clusters; they transport the nymphs and establish them at suitable feeding sites. The effect of these benefits is most marked when the ant population is high relative to that of the scale.

The silken shelters built by *O. longinoda* over *S. zanzibarensis* clusters protect the ant during adverse weather and may only incidentally benefit the scales.

S. zanzibarensis and other honey-dew-producing Homoptera are the major food source for *O. longinoda.* Other sources are sufficient to maintain only relatively low populations of the ant.

The level of the *S. zanzibarensis* population depends on the level of the attendant *O. longinoda* population. Scales providing honey-dew in excess of the requirements of an ant colony are killed.

The *O. longinoda* worker shows two distinct patterns of behaviour towards *S. zanzibarensis.* When it is not being attracted by the desire for honey-dew its behaviour resembles that adopted towards insects on which it normally preys.

Acknowledgements.

I am greatly indebted to Dr. F. J. Nutman, O.B.E., for his advice and encouragement and also for the trouble he took in obtaining facilities for the work. I should also like to express my thanks to Dr. W. J. Hall, C.M.G., and members of the Commonwealth Institute of Entomology for identifying many of the insect species. The present work was stimulated by the review "The association of ants with Aphids and Coccids" by Mr. G. E. J. Nixon, to whom I am indebted for valuable advice and for the loan of his review prior to publication.

References.

Barber, E. R. (1923). The Sugar-cane Mealy Bug and its control in Louisiana.—Bull. La agric. Exp. Sta., no. 185, 16 pp.

* Bünzli, G. H. (1935). Untersuchungen über coccidophile Ameisen aus den Kaffeefeldern von Surinam.—Mitt. schweiz. ent. Ges., **16**, pp. 453–593. (R.A.E., (A) **23**, p. 679.)

Carter, W. (1933). The Pineapple Mealy Bug, *Pseudococcus brevipes*, and wilt of pineapples.—Phytopathology, **23**, pp. 207–242.

Dutt, G. R. (1912). Life histories of Indian insects. IV. (Hymenoptera).—Mem. Dep. Agric. India (Ent.), **4**, pp. 183–267.

---

* Original not examined.

FLANDERS, S. E. (1945). Coincident infestations of *Aonidiella citrina* and *Coccus hesperidum*, a result of ant activity.—J. econ. Ent., **38**, pp. 711–712.

HERZIG, J. (1937). Ameisen und Blattläuse.—Z. angew. Ent., **24**, pp. 367–435. (R.A.E., (A) **26**, p. 195.)

HOUGH, W. S. (1922). Observations on two mealy bugs, *Trionymus trifolii*, Forbes, and *Pseudococcus maritimus* Ehrh. (Hom., Coccidae).—Ent. News, **33**, pp. 171–176. (R.A.E., (A) **10**, p. 416.)

IBBOTSON, A. & KENNEDY, J. S. (1951). Aggregation in *Aphis fabae* Scop. I. Aggregation on plants.—Ann. appl. Biol., **38**, pp. 65–78.

* KIRKPATRICK, T. W. (1927). The Common Coffee Mealybug (*Pseudococcus lilacinus*, Ckll.) in Kenya Colony.—Bull. Dep. Agric. Kenya, no. 18, 110 pp. (R.A.E., (A) **16**, p. 308.)

LUBBOCK, J. (1882). Ants, bees and wasps.—3rd edn. 448 pp. London.

*NEGI, P. S., MISRA, M. P. & GUPTA, S. N. (1930). Ants and the Lac Insect (*Laccifer lacca*).—J. Bombay nat. Hist. Soc., **34**, pp. 182–188. (R.A.E., (A) **18**, p. 385.)

NIXON, G. E. J. (1951). The association of ants with Aphids and Coccids.—36 pp. London, Commonw. Inst. Ent.

NUTMAN, F. J. & SHEFFIELD, F. M. L. (1949). Studies of the clove tree. I. Sudden-death disease and its epidemiology.—Ann. appl. Biol., **36**, pp. 419–439.

* PERKINS, R. C. L. (1913). Introduction, being a review of the land-fauna of Hawaii.—In Sharp, D. Ed. Fauna Hawaiiensis, **1**, pt. 6, pp. xli & ci.

PHILLIPS, J. S. (1940). Immature nutfall of coconuts in the Solomon Islands.—Bull. ent. Res., **31**, pp. 295–316.

SERRANO, F. B. (1934). Pineapple mealy-bug wilt in the Philippines.—Philipp. J. Sci., **55**, pp. 363–377.

SMITH, H. S. & ARMITAGE, H. M. (1931). The biological control of mealybugs attacking citrus.—Bull. Calif. agric. Exp. Sta., no. 509, 74 pp.

SMITH, M. R. (1942). The relationship of ants and other organisms to certain scale insects on coffee in Puerto Rico.—J. Agric. Univ. Puerto Rico, **26**, pp. 21–27.

STRICKLAND, A. H. (1947). Coccids attacking cacao (*Theobroma cacao*, L.) in West Africa, with descriptions of five new species.—Bull. ent. Res., **38**, pp. 497–523.

STRICKLAND, A. H. (1951). The entomology of swollen shoot of cacao. II. The bionomics and ecology of the species involved.—Bull. ent. Res., **42**, pp. 65–103.

WAY, M. J. (1953). The relationship between certain ant species with particular reference to biological control of the Coreid, *Theraptus* sp.—Bull. ent. Res., **44**, pp. 669–691.

WAY, M. J. (1954). Studies on the life history and ecology of the ant *Oecophylla longinoda* Latreille.—Bull. ent. Res., **45**, pp. 93–112.

---

* Original not examined.

WHEELER, W. M. (1927). The ants of the Canary Islands.—Proc. Amer. Acad. Arts. Sci., **62**, pp. 93–120.

WHEELER, W. M. (1934). Revised list of Hawaiian ants.—Occ. Pap. Bishop Mus., **10**, no. 21, 21 pp.

WOGLUM, R. S. (1919). How nature assists in mealy bug control.—Calif. Citrogr., **4**, p. 106.

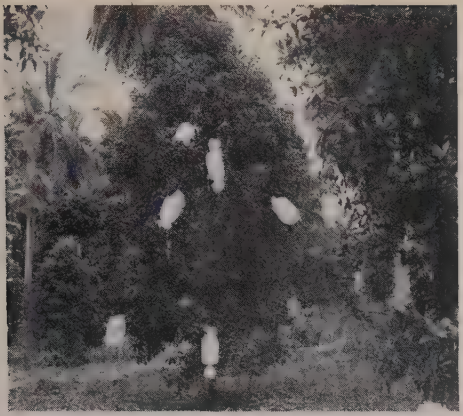


FIG. 1. Experiment to determine the effect on *S. zanzibarensis* of removal of attendant *O. longinoda*. Clusters of *S. zanzibarensis* on twigs of a young clove tree were caged. Half of the cages were left open to allow access of *O. longinoda;* the others were closed to exclude *O. longinoda*.

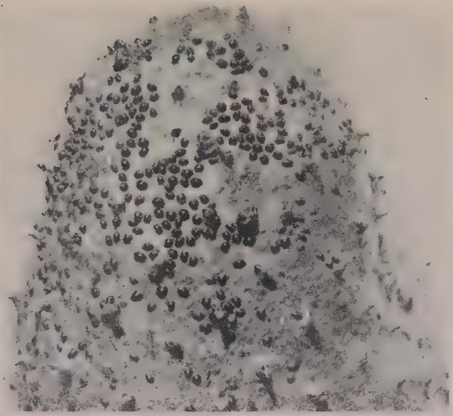


FIG. 2. *Saissetia nigra* tended by *O. longinoda* on a fruit of custard apple (*Annona muricata*). Two Lepidopterous larvæ covered with portions of cuticle of *S. nigra* which they have consumed can be seen.

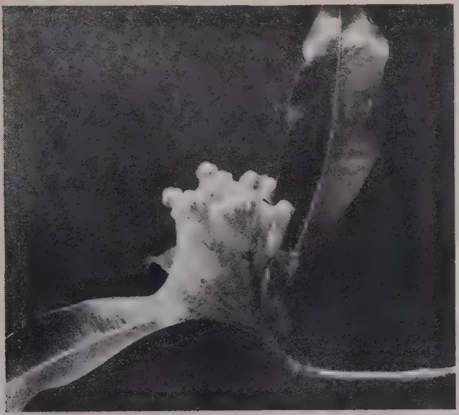


FIG. 3. Young inflorescence of the clove (*Jambosa caryophyllus*) infested with *S. zanzibarensis* and covered with a silken web built by *O. longinoda*.

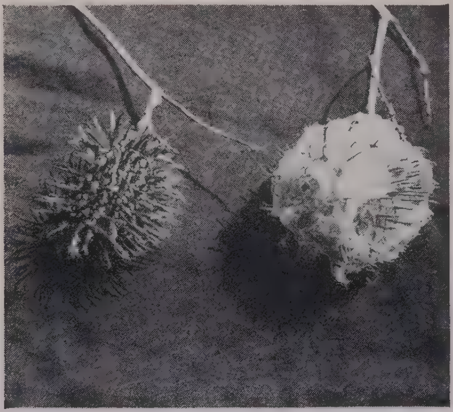


FIG. 4. Developing fruits of rambutan (*Nephelium lappaceum*). On the left, a normal fruit. On the right, a fruit infested with *S. zanzibarensis* and covered with a silken web built by *O. longinoda*.

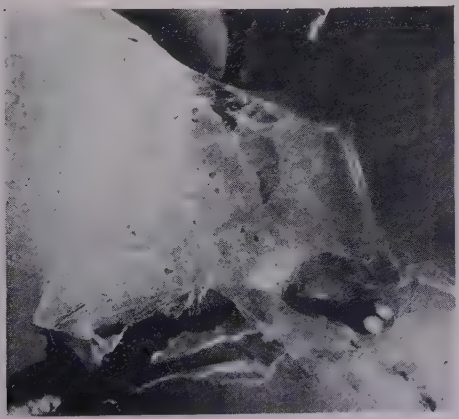


FIG. 5. Large silken web built by *O. longinoda* over *S. zanzibarensis* on developing coconut fruits.

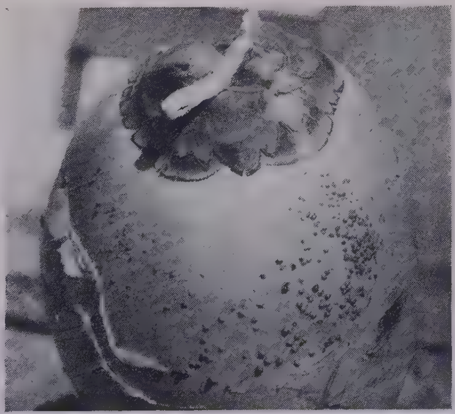


FIG. 6. Coconut fruit from fig. 5 with silken web removed to show adults and nymphs of *S. zanzibarensis*. Remnants of the attachment of the web can be seen.

AN ADDITIONAL NOTE ON THE FAUNA OF BIRDS' NESTS IN BRITAIN.

By G. E. Woodroffe.

Department of Scientific and Industrial Research,
Pest Infestation Laboratory, Slough, Bucks.

E.II.iv

In an earlier paper (Woodroffe, 1953) full details were given of the results of a survey, the purpose of which was to study the insects and mites which inhabit certain birds' nests in Britain. Since then further work has been carried out on certain species, and, as a result, one or two statements made in the earlier publication now require correction or modification.

1. *Ptinus subpilosus* Sturm (p. 747). This rare species has frequently been misidentified in the past, and the two records given, although checked by the British Museum (Nat. Hist.), now prove to have been based upon erroneous determinations. The female *subpilosus* is readily recognised, but the male is considerably more difficult. The characteristic thoracic "cushions" of *P. fur* (L.) are often hardly distinguishable on small male specimens. In such examples the rounded prominence which is situated between the oblique thoracic "cushions" is very conspicuous, and differs only in degree of development from the similarly situated tubercule of the male *subpilosus*. A careful comparison of external morphology and aedeagal structure has now been made between the two male specimens recorded as *subpilosus* and an authentic male of that species. As a result there can be little doubt that the two are diminutive and aberrant *P. fur*. Thus *P. subpilosus* must be deleted from the list of nest fauna (*cf.* Hinton, 1941 for taxonomy of *Ptinus* spp.).

2. *Ptinus hirtellus* Sturm. A single male *Ptinus* was found in a sparrows' nest in a private house at Gerrards Cross, Bucks., on 26.ii.52, but it was not then possible to identify it. It now appears probable that it was a male of *P. hirtellus*, although the separation of males of this species from male *P. latro* F. cannot be made with complete confidence (Hinton, 1941). *P. hirtellus* was not recorded from nests in the earlier paper.

3. *Ptinus fur* (L.) (p. 747). The question of the colonisation of nests by flying adults of nest-dwelling species was discussed previously in some detail. The position of the spider beetles was of considerable importance because of the variation in power of flight shown by the several species. An observation was described which illustrated that *P. fur* will fly under certain conditions, although its flight has seldom been observed. The degree of development of the membranous wings has now been studied in those species about which little was known of their powers of flight. It was found that fully developed, and therefore possibly functional, membranous wings were present in males only of *fur*, *hirtellus* and *subpilosus*. In male *pusillus* Sturm the wings were greatly reduced, and almost certainly functionless, and in the females of all four species the wings were vestigial. It is, of course, possible that fully-winged females of these species occur occasionally, but, of all the species of *Ptinus* recorded from nests, only *sexpunctatus* Panz. is normally fully winged in the female, and consequently none of the others are capable of colonising nests by flight, although the males, except *pusillus* and *tectus* Boie., may reach them in that way.

4. *Glycyphagus* n. sp. (p. 752). Miss P. L. Robertson has now identified this mite as probably *Glycyphagus geniculatus* Vitz. One doubt concerning

this determination is that *G. geniculatus* is not described as possessing the bright red lateral vesicles which were such a conspicuous feature of all examples which have been studied. However, in most other respects, the structural similarity was extremely close. Miss Robertson's account of this species is in preparation.

Acknowledgement.

This note is published with the consent of the Department of Scientific and Industrial Research.

References.

Hinton, H. E. (1941). The Ptinidae of economic importance.—Bull. ent. Res., **31**, pp. 331–381.

Woodroffe, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain.—Bull. ent. Res., **44**, pp. 739–772.

TEMPERATURE COEFFICIENTS OF INSECT KILL BY VOLATILE SOLID INSECTICIDES.

By A. H. McIntosh.

Department of Insecticides and Fungicides,
Rothamsted Experimental Station,
Harpenden, Herts.

E.M N

Commercial insect fumigants usually work best when the temperature of fumigation is rather high. But sometimes, especially at temperatures below 10°C., the coefficient of killing is negative, *i.e.*, lower temperatures give higher kills (Peters & Ganter, 1935; Moore, 1936; Shepard & others, 1937; Sun, 1947).

I have found that the two volatile solid chlorinated hydrocarbon insecticides DFDT [1 : 1-bis(*p*-fluorophenyl)-2 : 2 : 2-trichloroethane, m.p. 42–43°C.] and γ BHC [γ benzene hexachloride, m.p. 109·5–111°C.] can, rather unexpectedly, show negative coefficients in laboratory fumigation tests. DFDT gave negative coefficients with both the insect species used; γ BHC gave a negative coefficient with one species, and a positive coefficient with the other. A third compound, aldrin [1 : 2 : 3 : 4 : 11 : 11-hexachloro-1 : 4 : 5 : 8 : 9 : 10-hexahydro-1 : 4 : 5 : 8-*endo-exo*-dimethylene-naphthalene, m.p. 98–99°C.], gave positive coefficients with both species.

Method of Testing.

Oryzaephilus surinamensis (L.) was reared at 30°C. on rolled oats, and *Tribolium castaneum* (Hbst.) at 30°C. on wholemeal flour. With *O. surinamensis*, 50 adults were put in a 1-inch diameter glass tube, which was closed at the top with nylon parachute fabric and then placed in a petri dish beside some crystals of poison. With *T. castaneum*, 50 adults were put directly on the floor of the petri dish; the poison was in an open glass tube beside them. Each dish was closed by putting another one upside down on top, and sealing the two together, rim to rim, with cellulose tape (*cf.* Pradhan, 1949*b*). In this way the insects were exposed to air saturated with poison vapours at either 30°C. or 11°C. Neither species had any food.

Atmospheric humidity sometimes affects results of tests of contact poisons (Pradhan, 1949*b*). The humidity of the air in the dishes was unknown and probably not the same at each temperature. To make sure that the results were due to differences in temperature only, some tests were made on *O. surinamensis* at 100 per cent. R.H. by including a small open tube of water in each dish.

Results.

Every day for five days the dishes were opened at room temperature so that counts of kill could be made; and then the insects were put back in the vapours again at the same temperatures as before. After five days the kills in the controls were sometimes as high as 50 per cent., especially with *O. surinamensis*. The times for each treatment to give 50 per cent. and 90 per cent. corrected kill were found by the probit method, and are shown in pairs to the left of each column in Table I; the figures for 90 per cent. corrected kill are those in brackets. The probit line for the more toxic temperature was always slightly steeper. The tests were repeated several times; each of the figures represents the combined results from about 400 insects.

The pairs of figures to the right of each column are the ratios of times needed to give 50 per cent. (and 90 per cent.) corrected kill. Those in bold type show negative coefficients; the others are positive.

TABLE I.

Times for fumigant poisons to give 50% (and 90%) corrected kill, with ratios of speeds of action. Figures in bold type show negative coefficients of kill.

Species	Temp. °C.	DFDT (m.p. 42–43°C.)		γ BHC (m.p. 109·5–111°C.)		Aldrin (m.p. 98–99°C.)	
		Days	Ratios of speeds	Days	Ratios of speeds	Days	Ratios of speeds
T. castaneum	30	7·6 (17·1)	**2·1 (3·0)**	<1·0 (<1·0)	? (>1·7)	<1·0 (<1·0)	>1·7 (>2·
	11	3·7 (5·7)		<1·0 (1·7)		1·7 (2·4)	
O. surinamensis	30	4·8 (8·6)	**1·4 (1·7)**	5·0 (11·2)	**2·1 (2·9)**	3·0 (4·9)	2·3 (2·
	11	3·4 (4·9)		2·4 (3·9)		6·8 (14·3)	
O. surinamensis at 100% R.H.	30	7·3 (19·6)	**1·9 (2·6)**	4·8 (15·8)	**1·5 (3·1)**	4·1 (8·9)	1·4 (1·
	11	3·9 (7·5)		3·1 (5·1)		5·8 (16·8)	

Discussion.

(1) There are no published figures for the vapour pressure of DFDT. An increase in temperature from 11°C. to 30°C. increases the vapour pressure of γ BHC by 21 times (Balson, 1947), and affects its toxicity to the two species in opposite ways. In the same temperature range, aldrin has a vapour pressure increase of only 3 times,* but gives a positive coefficient with each species. There is clearly no simple general physical rule connecting the toxicity of any one compound with its vapour pressure or temperature.

(2) Because no tests were made at temperatures between 11°C. and 30°C., these results do not help to decide whether or not the so-called " vital optimum " temperature of an insect species is the same as its temperature of greatest resistance to poisons (Gösswald, 1934; Craufurd-Benson, 1938; Häfliger, 1949; Pradhan, 1949*a*). With *T. castaneum* for instance, it looks at first sight as if the temperature of greatest resistance is 30°C. or above for DFDT, and 11°C. or below for γ BHC or aldrin. But it is quite possible that the temperatures of greatest resistance to all three poisons may in fact be between 11°C. and 30°C. If so, they may not be very different from one another and may even be close to the " vital optimum " temperature.

(3) If a contact poison can act as a fumigant as well, any method for finding the coefficient of killing by contact action alone must either be rather complicated or must depend on subtraction of the fumigant action from the fumigant plus contact action.

(4) This work is a sideline based on some chance observations, and will not be taken further at Rothamsted.

---

* Figure from Shell Chemical Corp. (Julius Hyman Div.), Denver, Col., U.S.A.

Summary.

Three volatile solid insecticides (DFDT, γ BHC and aldrin) were tested against two species (*Oryzaephilus surinamensis* and *Tribolium castaneum*) at two temperatures (30°C. and 11°C.) in simple laboratory fumigation tests. DFDT killed both species faster at 11°C. than 30°C.; γ BHC killed *O. surinamensis* faster at 11°C. than 30°C., but *T. castaneum* faster at 30°C. than 11°C.; aldrin killed both species faster at 30°C. than 11°C.

Acknowledgement.

I would like to thank Mrs. Margaret Macfarlane for carrying out the tests, and for her suggestions for improving the method.

References.

Balson, E. W. (1947). Trans. Faraday Soc., **43**, pp. 54–60.

Craufurd-Benson, H. J. (1938). Bull. ent. Res., **29**, pp. 41–56.

Gösswald, K. (1934). Z. angew. Ent., **20**, pp. 489–530.

Häfliger, E. (1949). J. econ. Ent., **42**, pp. 523–528.

Moore, W. (1936). J. econ. Ent., **29**, pp. 65–78.

Peters, G. & Ganter, W. (1935). Z. angew. Ent., **21**, pp. 547–559.

Pradhan, S. (1949*a*). Bull. ent. Res., **40**, pp. 239–265.

Pradhan, S. (1949*b*). Bull. ent. Res., **40**, pp. 431–444.

Shepard, H. H., Lindgren, D. L. & Thomas, E. L. (1937). Tech. Bull. Minn. agric. Exp. Sta., no. 120, pp. 16–18.

Sun, Y. P. (1947). *Ibid.*, no. 177, pp. 59–64.

A PRELIMINARY STUDY OF THE *GLOSSINA PALLIDIPES* AUSTEN POPULATION AT MAKUENI, KENYA.

By S. G. Wilson.
*Veterinary Department, Kabete, Kenya.**

S. G.

The Makueni fly-belt of Kenya lies between Latitude 1° 30′ and 2° 00′ South, and Longitude 37° 30′ and 38° 00′ East. The country is broken and slopes eastwards from 4,000 ft. above sea level at Unoa and Campi ya Mawe in the west to 2,600 ft., approximately, on the Athi river in the east. It is drained by two main river systems, the Keite-Thwake rivers (fig. 1) in the north and the Kiangine-Kikuuni rivers in the south, both rivers flowing eastwards into the Athi river.

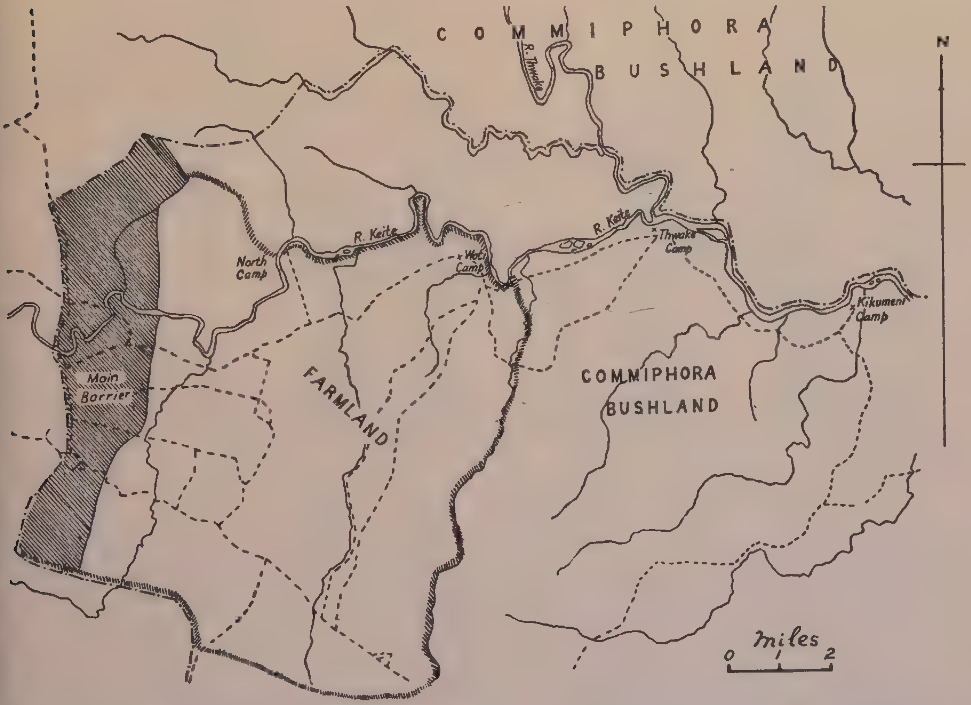

COMMIPHORA
BUSHLAND
R. Thwake
N
R. Keite
R. Keite
North Camp
Woti Camp
Thwake Camp
Kikumeni Camp
Main Barrier
FARMLAND
COMMIPHORA
BUSHLAND
miles
0
1
2

Fig. 1.—Sketch map of Makueni area showing situation of North, Woti, Thwake and Kikumeni camps along the Keite-Thwake rivers from which most of the data on *G. pallidipes* was collected.

The collection of routine data on the tsetse population in this area has been in progress since 1948. Weekly patrols have been carried out by trained African fly-boys along forty regular routes. These fly-boys can be relied upon to count and to record accurately the total flies caught, to recognise species, to distinguish between male and female flies, to "hunger stage" flies caught, and to distinguish between teneral and non-teneral flies. A considerable number of records on which to base this preliminary analysis is therefore available.

---

* Now Director of Veterinary Services, Northern Nigeria.

Climate of the Area.

The climate over the whole area is hot and dry, the highest day temperatures occurring during February–March and in September–October, and the lowest in July and August (figs. 2 & 3). Temperatures are naturally higher in the lower areas towards the Athi and Kiangine rivers where the average monthly maximum temperature usually exceeds 100°F. in February and March while at Woti or Unoa, towards the west, the equivalent temperatures seldom exceed 94°F.

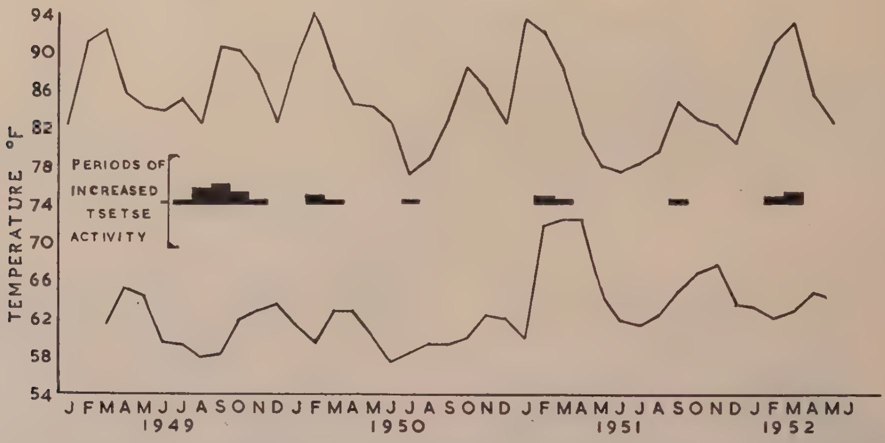


Fig. 2.—Average monthly maximum and minimum temperatures from January 1949 to June 1952 at Woti camp on the Keite river at an altitude of 3,500 ft. above sea level. Months of increased tsetse catches are also shown.

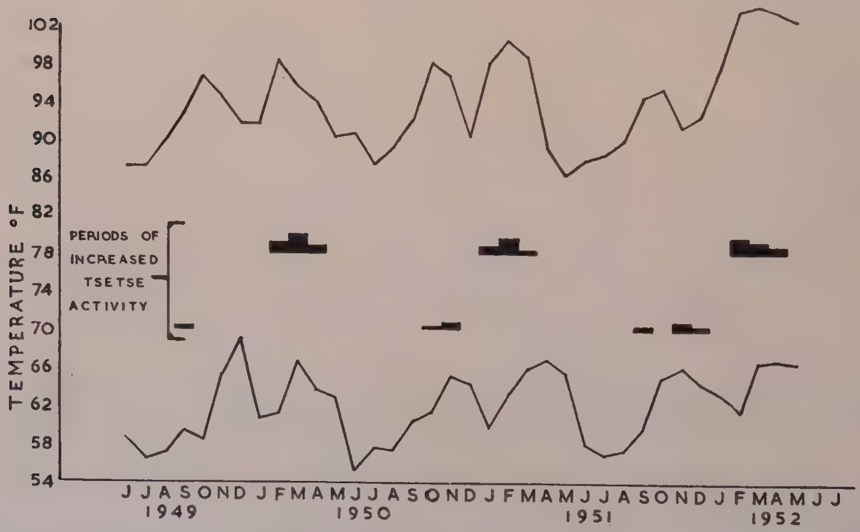


Fig. 3.—Average monthly maximum and minimum temperatures at Kiangine camp at an altitude of 2,500 ft. Months of increased tsetse catches are also shown.

There are two rainy seasons, the long rains occurring during March to May and the short rains during October and November. The area lies within the 20-inch rainfall belt but abnormally wet seasons may occur as in 1951 when 60·62 inches of rain fell as compared with 23·63 in. and 19·43 in. during 1949 and 1950 respectively (fig. 4). The amount of rainfall decreases from west to east, the driest areas being around the Athi river. The dry months of January and February are characterised by a high temperature and low humidity. During the long dry season from June to September, some rain or fine drizzle falls in July and August and temperatures are low.

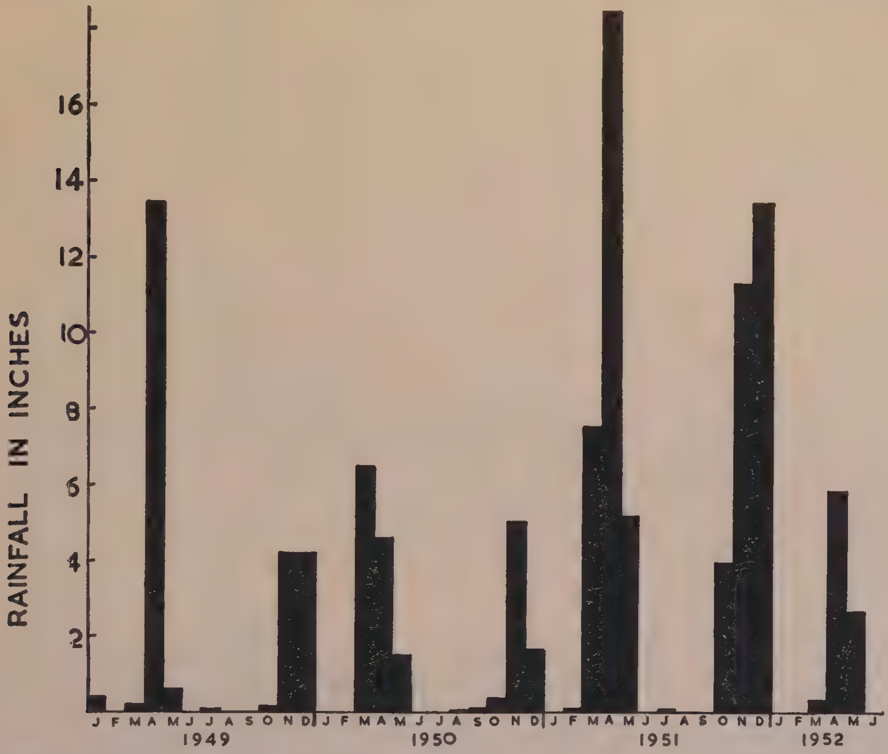


Fig. 4.—Total monthly rainfall at Woti camp during the period January 1949 to June 1952.

Vegetation.

The vegetation of the area may be broadly classified as complex *Acacia-Commiphora* dry grassland association. In the higher altitudes to the west, an *Acacia spirocarpa-Combretum* spp.-*Dalbergia melanoxylon* association is dominant, the associated species being *Lannea stuhlmannii*, *Commiphora pilosa*, *Acacia subalata*, *A. pennata*, *A. mellifera*, *A. senegal*, *Albizzia* sp., *Ormocarpum* spp. (2), *Grewia* spp., *Terminalia* sp., and many others of lesser importance.

In the country below 3,500 ft., east of the Keite-Thwake junction and along the Kiangine river, the vegetation is *Commiphora* dry scrub thicket. The tall trees are usually *Commiphora* spp., *Balanites aegyptiaca*, *Sterculia* sp., *Euphorbia* sp., *Erythrina burttii* and *Acacia mellifera* around which occur dense thickets consisting of *A. pennata*, *Combretum exalatum*, *Grewia* spp., *Thylachium africanum*, *Capparis kirkii* and *Salvadora persica*. These thickets are often associated with dense clumps of *Sansevieria robusta*. Between the thickets are open patches of grassland consisting chiefly of *Cenchrus ciliaris*, *Chloris myriostachya*, *Heteropogon contortus*, *Brachiaria* sp., *Panicum* sp., and *Eragrostis* sp.

Along the Keite, Thwake and Kiangine rivers, the narrow strip of alluvial soil forming the river banks, seldom more than 100 feet wide, supports at irregular intervals groups of tall trees of *Acacia*, *Mimusops*, *Ficus*, *Piptadenia* and *Delonix elata*. A dense undergrowth of tall woody shrubs occurs in places, consisting chiefly of *Craibia*, *Anisotes*, *Cordia* spp., and *Salvadora persica*.

The changes in this vegetation closely follow the rainy seasons. During January and February, in the deciduous *Commiphora* thickets below the 3,500 ft. contour, the trees are leafless and most shrubs are dry and wilting. The riverine vegetation, and to a lesser extent the *Combretum* associations to the west, remain relatively green. With the onset of the rains at the end of February or early in March, the trees and most shrubs take on new leaves and become green and shady and remain so throughout April and May. In June, the *Acacia* spp., especially *A. mellifera*, drop their leaves and the grasses commence drying up so that in July most of the *Commiphora* trees are leafless and the shrubs in the thickets, including *Combretum exalatum*, begin to wilt and lose their leaves. During August and September the only trees retaining leaves and affording some shade are found in the *Combretum-Dalbergia* communities on the higher ground west of Woti camp but more especially amongst riverine vegetation. The rest of the country is bare and leafless and grass fires commonly occur.

During the short rains in October, vegetation springs again into leaf and most trees, including *A. mellifera*, *A. pennata*, *Commiphora* spp., *Adansonia digitata* and *Ficus* sp., are in leaf. They usually remain in leaf during November and December and there is a luxuriant growth of grass.

There are therefore two dry leafless periods, one during January and February associated with high temperatures and the other during August and September when temperatures are cooler.

Game Present in the Area.

The Makueni area has always been one favoured by rhinoceros and before any settlement was possible east of Unoa Hill over 1,000 head were shot in 1948. Many still remain especially around Kikumeni and Kiangine and Athi localities. Herds of elephant and buffalo are also much in evidence in certain seasons. In addition, all the usual smaller game are present such as impala, kongoni, hartebeest, duiker, bush-buck, lesser kudu and dik-dik. Zebra, giraffe, eland and roan antelope are only occasionally seen.

The System of Patrols in Operation at Makueni.

The three species of *Glossina* which occur at Makueni are *G. pallidipes* Aust., *G. longipennis* Corti and *G. brevipalpis* Newst., but the first-named species is by far the most numerous and important tsetse and is the only one considered in this paper. Data on this fly population have been collected from eight fly camps permanently staffed by African fly-boys who work under European supervision. These camps are scattered over an area of 250 square miles but most of them are adjacent to the main rivers. Thus North Camp, Woti, Thwake, Kikumeni and Athi camps are along the northern river system, the Kiangine camp is in the south while only the camps at Campi ya Mawe and at Thabu cover the inland *Commiphora* bushland.

Patrols have been carried out by two men using a blackened cloth screen 6 ft. × 3 ft., the flies being caught with hand nets as they alight on the screen, and to a lesser extent from nearby vegetation. No bait oxen patrols have been used so that results throughout the area might be as uniform as possible.

Patrols moved along definite marked paths which at first were irregular in length but later were standardised at 6,000 yd. long. Each patrol path was

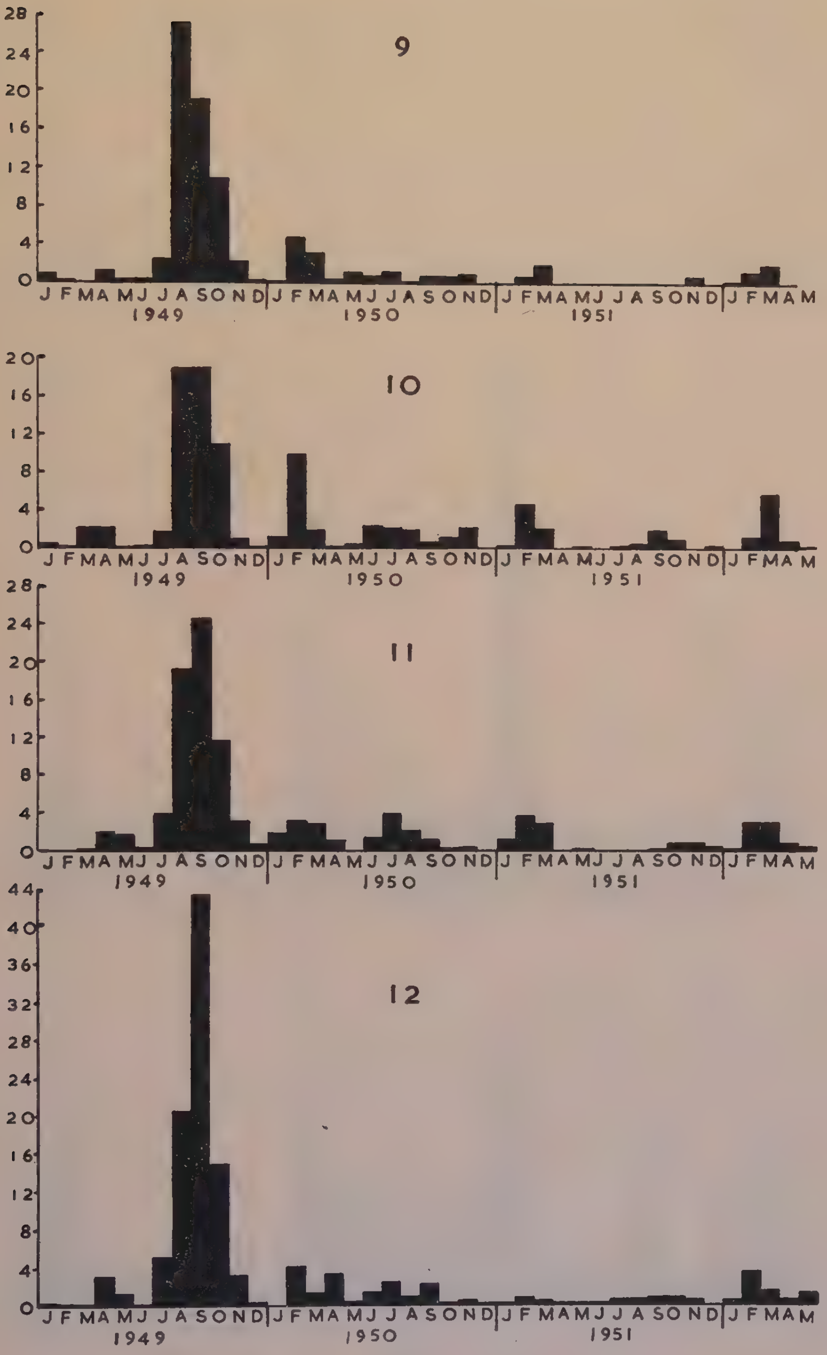


Fig. 5.—Average number of *G. pallidipes* caught per patrol along patrols nos. 9, 10, 11 and 12 during each month from January 1949 to May 1952.

traversed once each week or four times per month, two of the patrols being carried out in the morning and two in the afternoon. These patrol routes were not subdivided into sections nor were they specially designed to investigate any apparent density in the various types of vegetation. The flies caught therefore were taken to represent the apparent density of the population in the area as a whole and not in any small specialised locality.

The patrol paths along the Keite-Thwake rivers run either along or adjacent to the river bank or else traverse thickets likely to hold *G. pallidipes* at no great distance from the river. The inland patrols based at Campi ya Mawe have for some years caught so very few flies that the data are of little significance while the second inland camp at Thabu was only started in December 1951.

Owing to the uncertainty of what would happen, there was a lack of a basic design in these patrols and the interpretation of the results is therefore not always

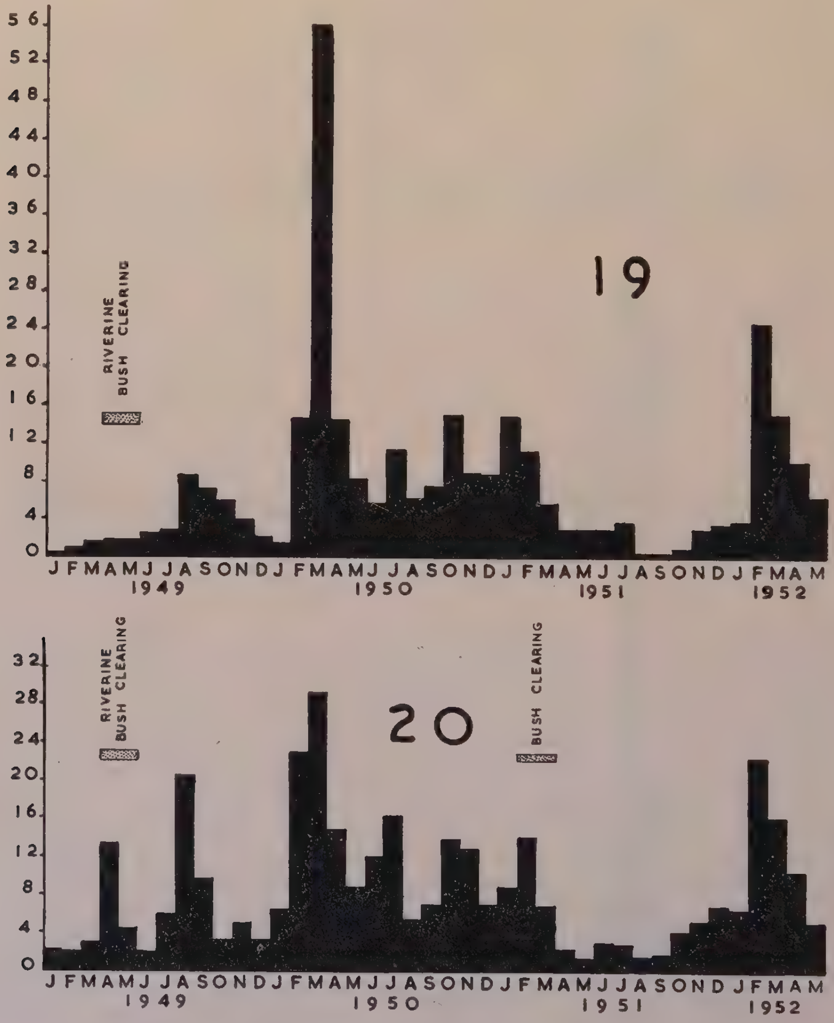


Fig. 6.—Average number of *G. pallidipes* caught per patrol along patrols nos. 19 and 20 at Thwake camp.

easy. It must also be remembered that by our patrol system we collected a small and possibly an abnormal sample of the total *G. pallidipes* population in that the flies caught were nearly always hungry and often died soon after catching. In spite of these limitations, however, the results of patrols should reveal gross changes in the fly population.

Total Flies Caught along Regular Patrols.

Since so little is known of the behaviour of *G. pallidipes* under the climatic conditions experienced at Makueni, the total flies caught by patrols were first examined, irrespective of the age or sex of the flies. The average number of flies caught per patrol each month from January 1949 to May 1952 for five groups of patrols working along the Keite-Thwake rivers is shown in figs. 5 to 9.

Patrols nos. 9, 10, 11 and 12 (fig. 5) operate in the western areas, nos. 9 and 10 being on the north bank and nos. 11 and 12 on the south bank of the Keite river. The area covered by these patrols is now largely occupied by African settlers, so high catches of *G. pallidipes* were not expected. Patrols nos. 19 and 20 (fig. 6) and nos. 21 and 22 (fig. 7) operate from the Thwake camp at the

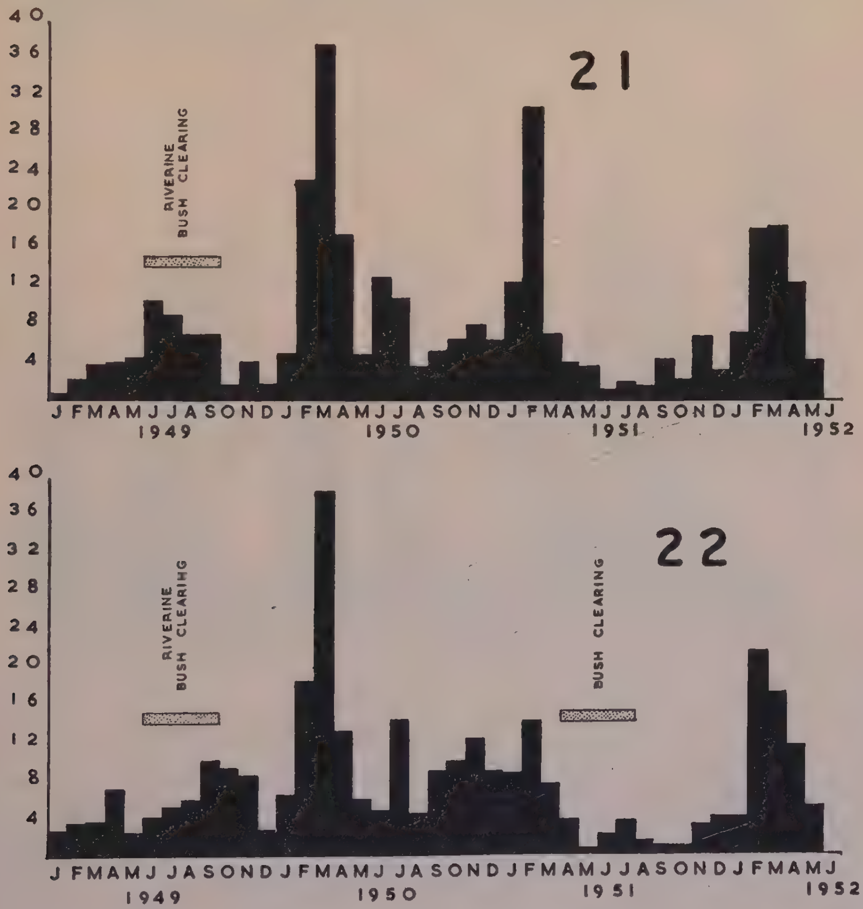


Fig. 7.—Average number of *G. pallidipes* caught per patrol for each month along patrols nos. 21 and 22 working from Thwake camp.

junction of the Keite-Thwake rivers and the only alteration in the vegetation in this area was the 200-yard riverine clearing carried out in 1949. The areas covered by patrols nos. 25 and 28 (fig. 8) and nos. 29 and 30 (fig. 9) operate further to the east, from Kikumeni camp on the Keite river, and here the vegetation has remained entirely untouched by human interference.

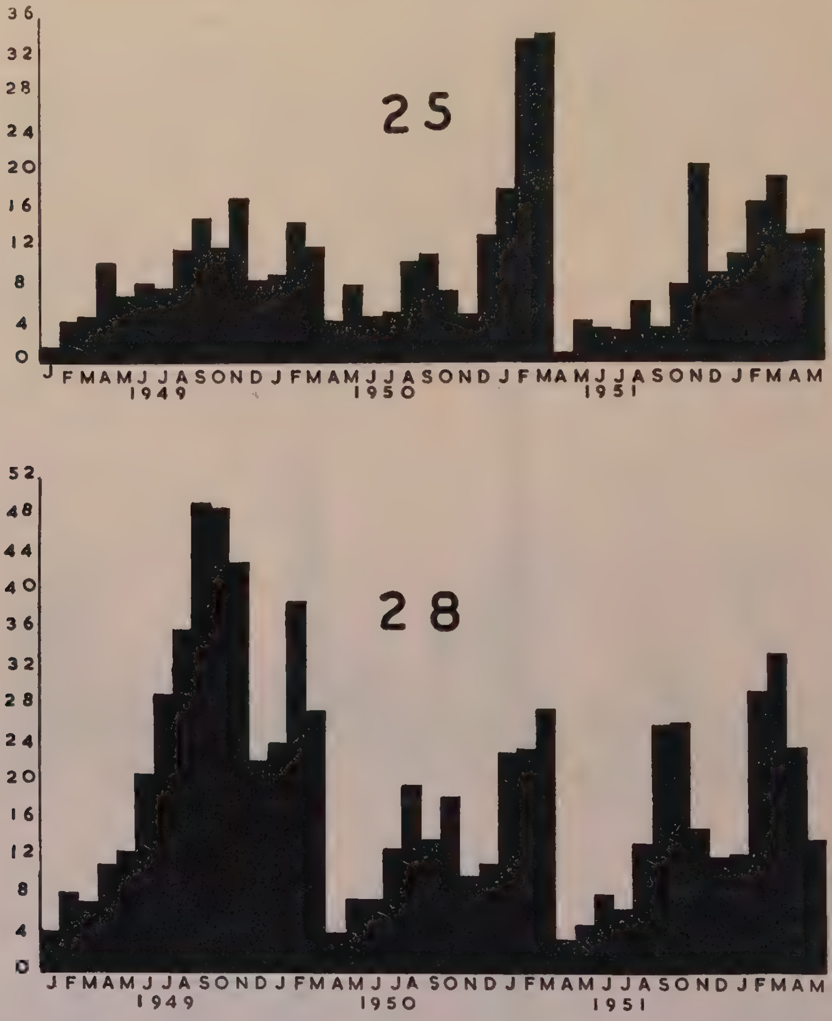


Fig. 8.—Average number of *G. pallidipes* caught per patrol for each month along patrols nos. 25 and 28 working from Kikumeni camp.

The most constant seasonal feature shown by all patrol returns is the marked increase in the numbers of *G. pallidipes* caught during the months of February and March of each of the three years 1950–52. The magnitude of this rise varied with the locations of the patrols, being naturally less evident along patrols in the cleared settled areas (fig. 5) than along patrols downstream in areas with wide hinterlands of densely infested bush and where tsetse populations are generally high (figs. 6 to 9).

This February–March rise in fly numbers was highest during 1950 along all patrols operating from Thwake camp and westwards (figs. 5, 6 & 7), the rise being spectacular along patrols nos. 19 and 22. Further eastwards, downstream along the Thwake river, the highest increase along patrol no. 28 occurred in 1950, along patrol no. 25 in 1951, and along patrols nos. 29 and 30 in 1952.

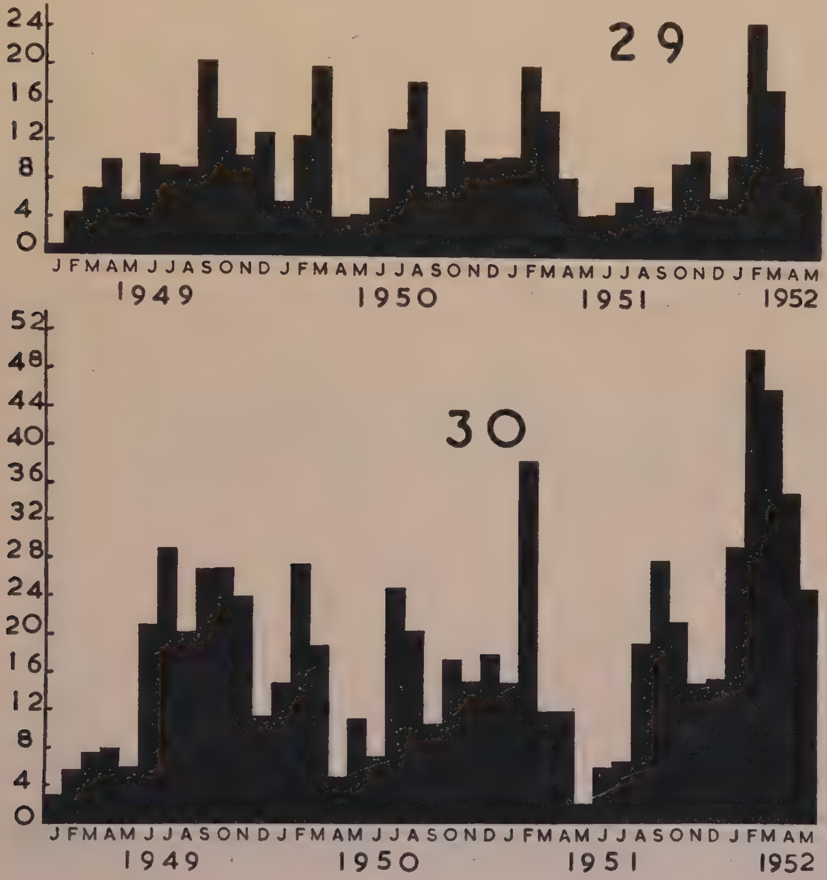


Fig. 9.—Average number of *G. pallidipes* caught per patrol along patrols nos. 29 and 30 working from Kikumeni camp.

Following the increase in February and March, a decrease in flies caught was experienced either in April, May or June. This decrease in turn was almost invariably followed by a second seasonal rise in flies caught during June, July and August. Examination of this July rise shows that in 1949 it was unusually intense. The rise occurred in July and the flies became so numerous and obvious, especially in the settled areas (fig. 5), that it became known as an "invasion." In the settled areas west of Woti the rise in catches was first noticed in July, was most marked in August, September and October and catches did not reach normal figures until December (fig. 5).

This July rise in 1949 was, however, less marked along patrols working from the Thwake camp although in each case a definite rise did occur at the same time as in the settled area (figs. 6 & 7). In the patrols downstream at Kikumeni (figs. 8 & 9) a rise was first noticed in June 1949 and was prolonged, as for example along patrol nos. 28 and 30 where catches were abnormally high from June until the end of the year.

The June–July rise was again noticed in 1950 but decreased without becoming of " invasion " dimensions and a third rise occurred in October and November, while in 1951, along most patrol routes, catches of *G. pallidipes* from April onwards were abnormally low and no second or third seasonal rises could be detected.

If we assume for the moment that 1950 was a more or less normal year we may, under Makueni conditions, expect a rise in the total flies caught during February and March with less marked rises during June or July, and again during October or November. In a year like 1949, the two latter rises may form one continuous abnormal increase in population. In 1951, under a different set of circumstances, the same two rises may not be detectable in some areas and the fly catches may remain abnormally low for the second half of the year.

Average Number of Old Males per Patrol.

It is usual to represent the apparent density of a tsetse population by the number of non-teneral males caught per 10,000 yards. The average number of old males caught per month along patrols of 6,000 yards is shown in figs. 10 to 13. If these catches are compared with those shown in figs. 6 to 9, it is evident that the chief population trends shown by the total catches are again reflected in the average total of old males caught per patrol.

The returns from patrols nos. 19, 20, 21 and 22, working from Thwake camp are given in figs. 10 and 11. It is again evident that 1949 was an unusual year

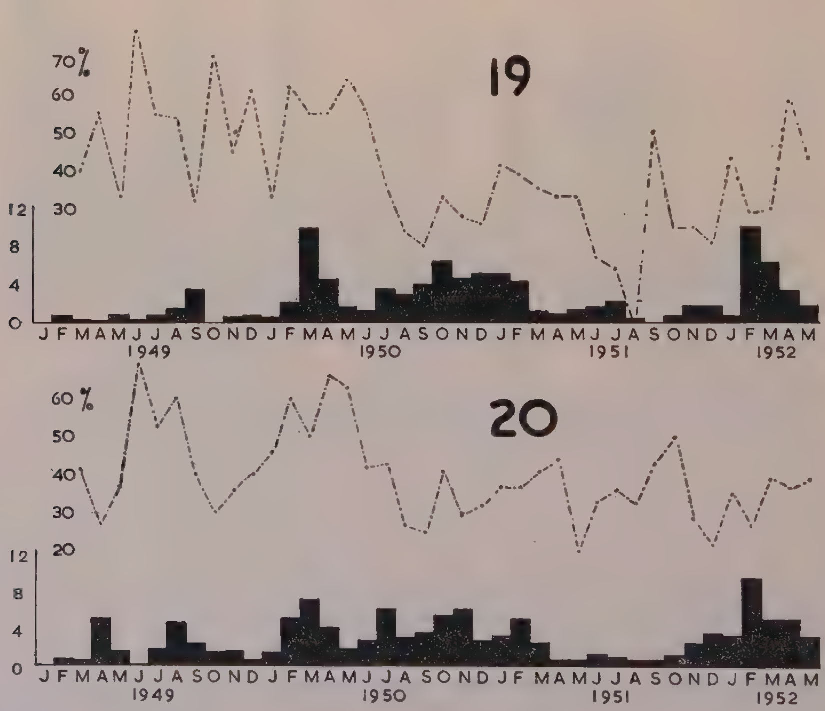


Fig. 10.—Average number of old male *G. pallidipes* caught per patrol each month along patrols nos. 19 and 20 and also the percentage teneral flies in catches each month.

in that no February–March rise occurred and signs of the invasion in the second half of the year are evident although on a very much reduced scale. Also the uniformly high catches for 1950 are again shown with a rise during February and March, a decrease in May and June and a more or less uniform figure of 4 males per 6,000 yards during the latter half of the year. Again, however, in some patrols there was a fall in catches during August (fig. 11) so that catches during the latter half of the year might be divided into two portions showing a rise during June and July, and a third rise during September to December.

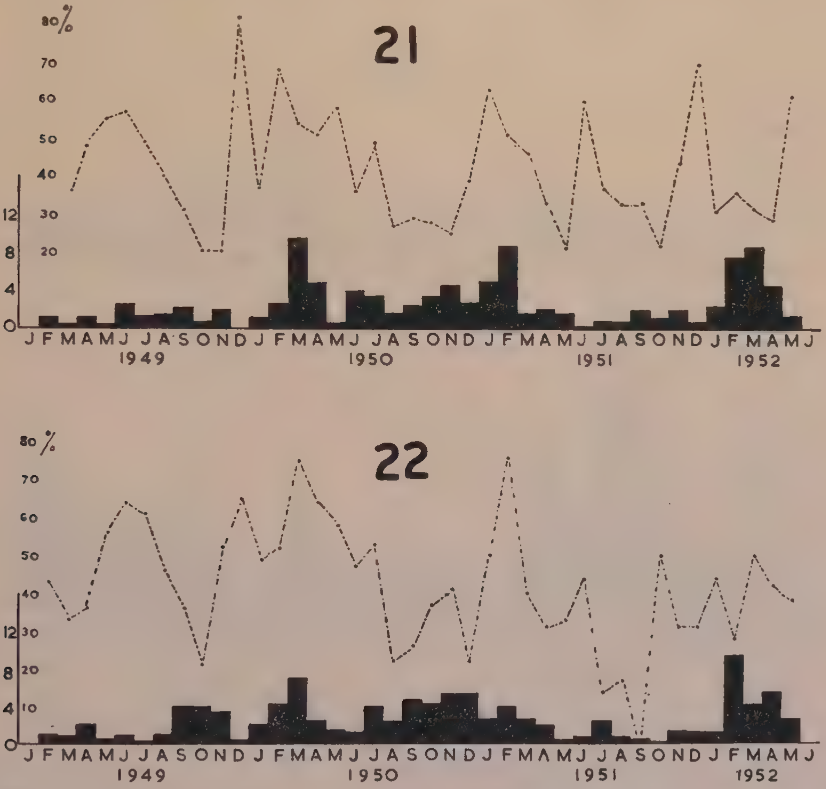


Fig. 11.—Average number of old male *G. pallidipes* per patrol each month along patrol routes 21 and 22 and also the percentage teneral flies in each monthly catch.

The low catches of old males during 1951 (figs. 10 to 13) are again similar to those shown in figs. 5, 6 and 7, with the February and March rise usually as the most striking feature of the year's catches. The returns for old males caught in 1952, although incomplete, show that the usual February and March rise occurred along all patrols even in the settled areas.

Along the patrols working from Kikumeni (figs. 12 & 13) there was again no rise in catches during February and March 1949, but the evidence for the rise in catches for June 1949 onwards is very striking especially along patrols nos. 28 and 30. The returns for 1950 show all the usual features but, contrary to that which was found at Thwake, the 1951 catches were as high if not higher than the numbers caught during 1950. The rise in catches during the early months of 1952 is again impressive.

Proportion of Teneral Flies in Monthly Catches.

The percentage of teneral flies for each month along certain patrols is also shown in figs. 10 to 13. Comparing the proportion of teneral flies in catches at Thwake camp (figs. 10 & 11) with those at Kikumeni (figs. 12 & 13) it is evident that the percentage of tenerals is higher at Thwake. At this camp the range is from 20 to 65 per cent., while at Kikumeni the range is smaller and for the greater majority of months falls between 15 and 35 per cent.

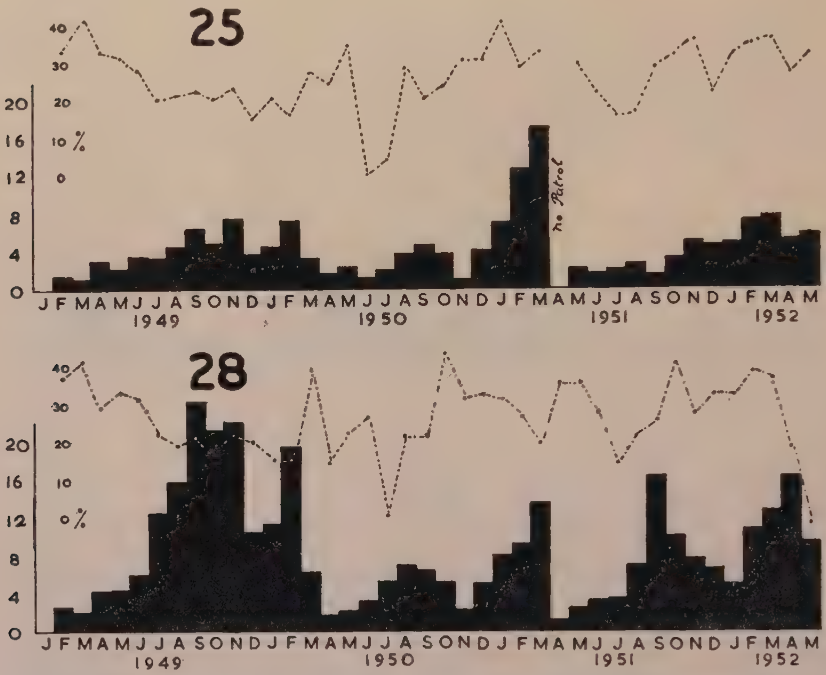


Fig. 12.—Average number of old male *G. pallidipes* caught per patrol each month along patrols nos. 25 and 28 with the percentage teneral flies in each monthly catch.

At Thwake camp along patrols 19 and 20 (fig. 10) the percentage of teneral flies was highest from June 1949 to May 1950 and thereafter fell and seldom rose above 45 per cent. Actually along all four patrols nos. 19, 20, 21 and 22, there is a gradual fall throughout the year 1950 from a peak of over 70 per cent. tenerals in catches during the first few months of the year to below 30 per cent. in December. In 1951 there is a certain regularity in the increases of tenerals along patrol no. 21 which is less constant in patrol no. 22. In patrol no. 21 (fig. 11) the greatest numbers of tenerals were caught during January, June and December 1951 while during the same year in patrol no. 22 it occurred in February, June and October.

The rise and fall in the percentage of tenerals in the patrols operating from Kikumeni (patrols 25, 28, 29 and 30) is so irregular that no definite deductions can be made.

It is evident, however, from an examination of the records of all patrols from both camps that there was no equivalent rise in the percentage of teneral flies to correspond with the constant seasonal rise in total flies caught during February and March. Also during the "invasion" in the latter half of 1949, there was again no definite equivalent rise except possibly along patrol no. 20; but on this patrol a similar rise occurred during April and May of 1950 which was unconnected with any invasion. Fluctuations of a more irregular nature were also noted in the percentage of tenerals along patrol no. 19. At Kikumeni, where the increase in total flies and of old males caught was marked (particularly in nos. 28 & 30), the percentage of teneral flies caught actually decreased. This corresponds to observations actually made at the time of invasion when it was noted that the majority of flies caught were non-teneral with females slightly predominating.

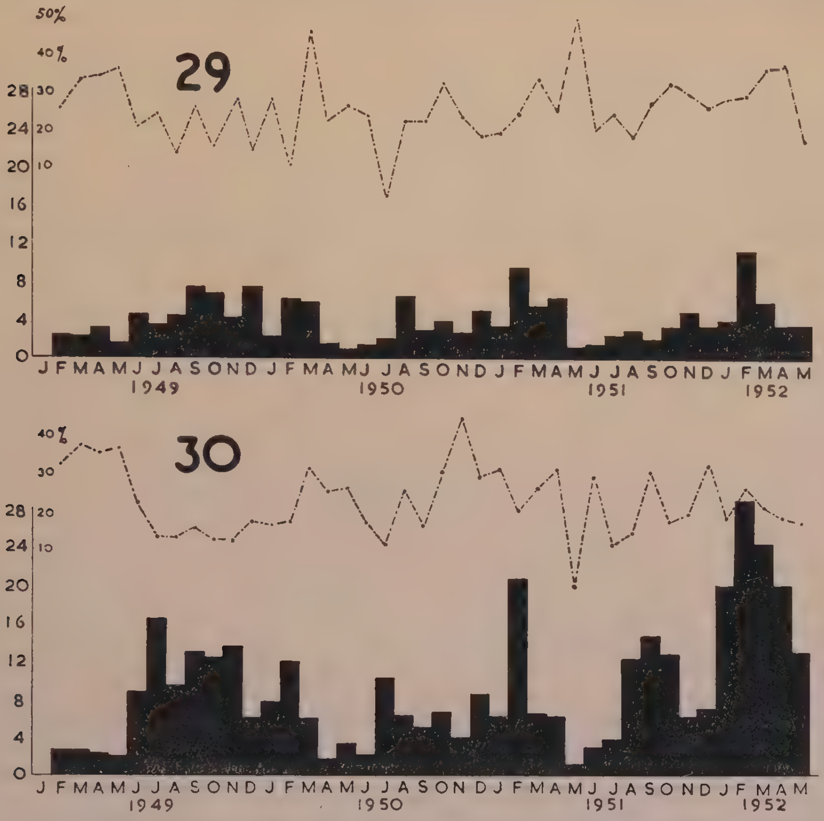


Fig. 13.—Average number of old male *G. pallidipes* caught per patrol each month along patrol routes 29 and 30 with the percentage teneral flies in each monthly catch.

Percentage of Males amongst Flies Caught.

The percentage of males in catches along four patrol groups is shown graphically in fig. 14. Patrols operating from Thwake camp are given in two groups, group K representing patrols nos. 19, 20, 23 and 24 while L represents patrols nos. 21 and 22. In these two groups more males than females were usually caught, the percentage of males caught being generally highest in 1951 and lowest in 1949, and only during the latter year did the number of males fall below 50 per cent. and then only for two months in group K and for four months in group L. The highest percentage recorded was 77 per cent. during July and October 1951 in group L.

The patrols grouped under M and N operated from Kikumeni camp, the M group representing the combined results from patrols nos. 25, 26, 27 and 28 while N represents patrols nos. 29 and 30. The percentages of males caught in both groups was generally lower than those found at the Thwake camp. During 1950 the percentage of males caught from March onwards was generally below 50 per cent. in both groups L and M. In 1949, apart from low figures for February and March, the percentage was generally between 50 and 60 per cent. In 1951 the percentage was generally higher than in 1949 and 1950 but only for one month did it exceed 65 per cent.

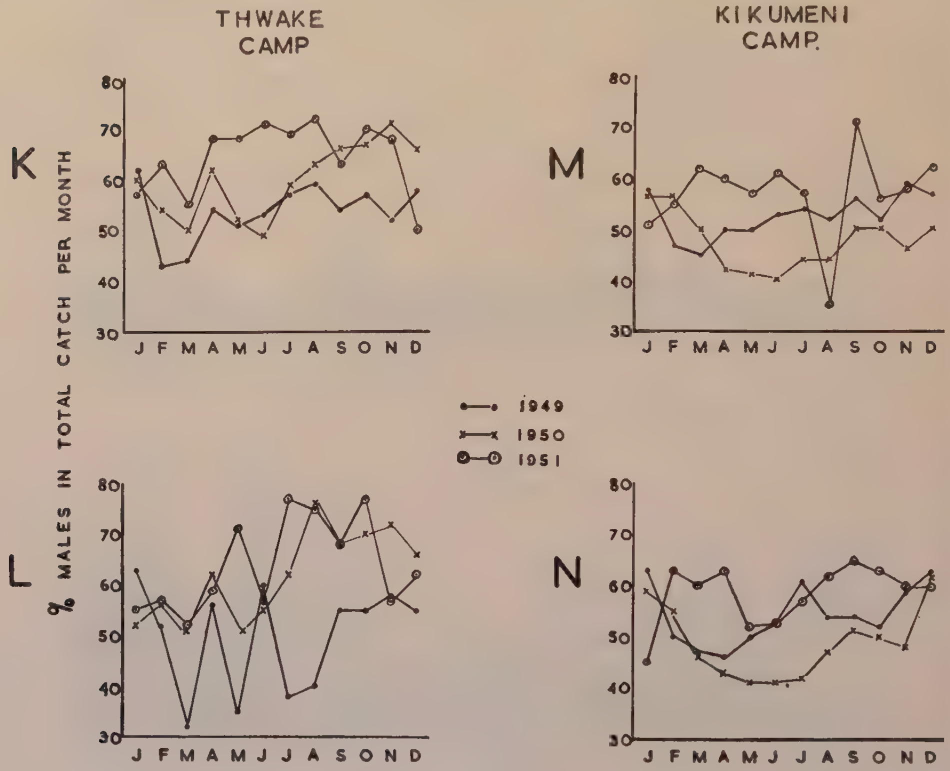


Fig. 14.—Graphs showing the percentage males in the total monthly catches of *G. pallidipes* at the Thwake and Kikumeni camps.

In general it can therefore be said that around Kikumeni, female *Glossina pallidipes* on many occasions formed the greater proportion of the catches and they were generally more numerous in catches in this area than round Thwake camp.

Discussion of these Results.

We have as yet no definite experimental data on the climatic and physiological causes behind the seasonal fluctuations and changes in composition of a *G. pallidipes* population. The February–March rise along the Keite-Thwake river patrols occurs *before* the heavy rains commence as shown in Table I.

A close correlation occurs between these rises and the maximum temperature curve since in every year in every locality, except for the abnormalities seen in 1949, the maximum catches occur when day temperatures are highest (figs. 2 & 3).

The increase in catches is such that it can only be accounted for by an influx of tsetse from outside sources. There is no evidence of major fly movements up or down-stream since rises always occur at one and the same time no matter how the patrol is located along the river, whether in the settled area in the west or the dense thickets in the east.

TABLE I.

Total *Glossina pallidipes* caught each week during January–March 1952 in relation to rainfall.

Week no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Rainfall each week (in.)	0·35	—	—	—	—	—	0·02	—	—	—	—	—	—	1·04

Total *G. pallidipes* caught each week.

Patrol no.														
21	8	18	1	2	18	19	11	25	23	27	19	5	19	19
22	5	3	3	5	23	27	6	30	11	14	27	17	24	14
23	7	10	6	1	14	22	25	20	11	21	25	9	18	13
24	6	13	9	18	21	24	18	28	12	20	40	31	30	12
25	7	14	12	12	15	19	14	18	16	25	13	21	19	16
26	7	10	14	11	15	14	50	9	21	20	21	16	18	13
27	5	12	17	12	17	9	11	10	20	19	7	20	13	8
28	13	14	11	12	27	26	42	23	25	21	54	34	33	14

During February and early March the *Commiphora* scrub away from the rivers is dry and leafless and must therefore provide the minimum shade for tsetse during the hottest time of the year. The riverine bush can, however, still provide some shade and the relative humidity is higher. The February–March rise may therefore represent an inward move of tsetse from the dry hot leafless thicket country towards the relatively shady riverine bush. This movement may also be influenced by movements of game which, during this dry period of the year, must visit frequently the only available water-holes along the larger rivers.

This suggested inward movement of tsetse receives some support from the study of the breeding sites of *G. pallidipes* on the Kiangine river. (Wilson, 1952; Parsons, 1954.) Along this river increased use was made of riverine breeding sites during the hot dry months followed by decreased use during the rainy months. There is no reason to doubt that this change in the use of riverine breeding sites bore some relation to tsetse movements towards and away from the riverine vegetation communities.

This preference of *G. pallidipes* for riverine areas rather than for thickets during the hot dry season is also shown by the returns from patrols 9, 10, 11 and 12 (fig. 5). During February–March the increase in flies caught is less marked along patrols nos. 9 and 12, some little distance from the river as compared with the riverine patrols 10 and 11, especially during the years 1951 and 1952. As will be noted later the 1949 August–September invasion of fly affected equally all these four patrols.

Moggridge (1936) under more extreme conditions in Italian Somaliland found that in the dry season *G. pallidipes* was restricted to the deciduous belt of thicket along the river bank. During the wet season when the scrub was in full leaf and shade, and humidity had increased, the fly dispersed outwards to a distance of 6 miles.

The patrols at Thabu were established in 1951 to throw some light on what actually happens to a *G. pallidipes* population in *Commiphora* bushland throughout any one season. The average catch per patrol (fig. 15) on two patrol routes nos. 48 and 49, which are shown on a map (fig. 16), illustrate this point.

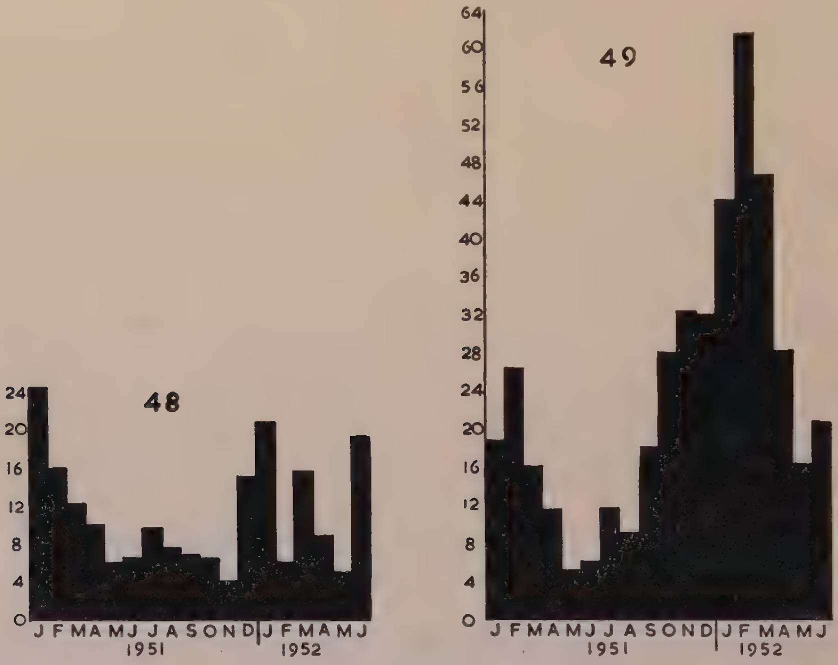


Fig. 15.—Average number of *G. pallidipes* caught per patrol each month along patrol routes nos. 48 and 49 working from Thabu camp.

Patrol no. 48 is entirely non-riverine, running on the higher ground east of the Kiangine road, and except for one patch of *Commiphora* thicket, there is little variation in the vegetative types along the route. The trees forming an open orchard country are chiefly *Commiphora* spp., *Acacia spirocarpa*, *Erythrina* sp., *Fagara* sp., *Balanites aegyptiaca*, *Acacia mellifera* with occasional *Boscia* and *Combretum* spp. The shrubs consist of *Acalypha*, *Premna*, *Thunbergia*, and *Coleus* spp., with occasional *Capparis kirkii*, *Grewia* spp., and rare patches of *Acacia pennata-Sansevieria* thicket. There is poor grass cover.

Patrol no. 49 runs for half its length along the Chunyu river, along the banks of which the trees form a two-storied canopy. The larger trees 30 to 40 feet high consist of *Commiphora* spp., *Lannea stuhlmannii*, *Ficus* spp., *Dombeya* sp., *Haplocoelum* sp., and a large riverine species of *Combretum*. Underneath these trees grow various shrubs consisting of *Croton* sp., *Acalypha* spp. (2), *Grewia* spp., *Combretum exalatum*, *Abrus* sp., *Craibia* sp. (very common), *Capparis kirkii* and *Phyllanthus* sp. with tall grasses. In the bushland adjacent to the river banks are found *Acacia spirocarpa*, *A. subalata*, *A. senegal*, *Boscia* sp., *Albizzia anthelmintica* with a few thicket patches of *Lasiosiphon*, *Croton*, *Grewia* spp., and *Entada flexuosa* with good grass cover.

Examination of the average total catches per patrol each month along these two routes during 1951–52 show that increases and decreases followed an identical pattern in both patrols during March–August 1951 (fig. 15). During September, October and November 1951 catches decrease in patrol no. 48 while they increase along patrol no. 49. June, July, August and September were dry months but the weather remained relatively cool until September when it became considerably hotter. During this hot dry month, therefore, fly appeared to desert the open *Commiphora* bushland of round no. 48 and to concentrate along the riverine vegetation of round no. 49 and this preference continued throughout the short rains of October and November.

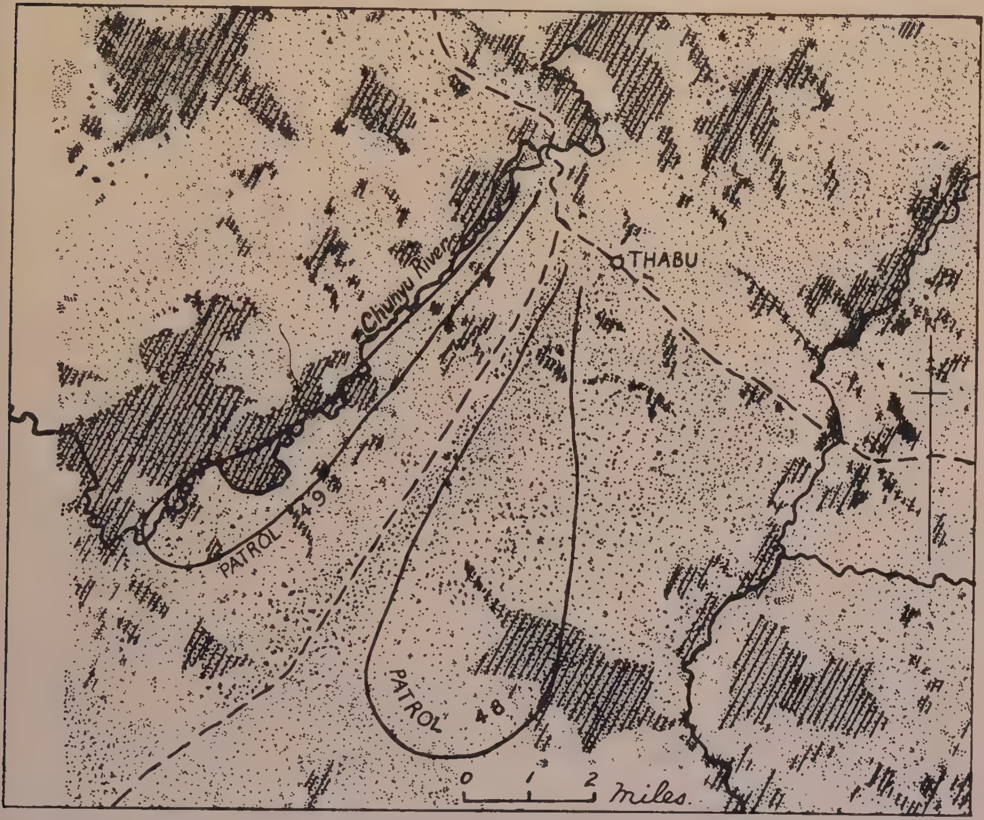


Fig. 16.—Showing routes of patrols 48 and 49 working from Thabu camp south of Makueni. Closed bush thickets are shown by shading and open bush-land by scattered dots.

During December 1951 and January 1952 there were increased catches along both patrol routes but the increase in no. 49 was proportionately much greater. There was some rain in December and while January was hot and dry, the bush was still leafy with some shade.

During February 1952 the weather continued hot and dry and most of the non-riverine trees and shrubs were leafless and this month offers the greatest contrast in the numbers of flies caught. Flies became very scarce along round no. 48, falling to an average catch of 6 flies per patrol but they increased along round no. 49 to the record high average catch of 61·5 flies per patrol or a total fly catch of 246 flies during the 4 patrols carried out in February. The catches for March to June again form a similar pattern in both patrols, decreasing gradually to a low level in May with some increase in June.

No reason why the February and March rises did not occur along patrols in the Thwake-Keite area in 1949 can be given, but fly patrols in all these areas had only then been established and it takes some little time to get African fly-boys accustomed to the work. It is therefore possible that the results during the early months 1949 were not entirely complete.

The high temperatures prevailing early in the year must cause some mortality and decrease in fertility in *G. pallidipes*, especially when temperatures above 98°F. (34·4°C.) are recorded for several days and weeks. This may account to some extent for the fall in fly catches during the following months of May and June of each year. On the other hand, it may be due chiefly to a wider dispersion of *G. pallidipes* population throughout the *Commiphora* and *Combretum* thickets and woodlands owing to the cooler day-temperatures in these latter months and to the leafy, shady nature of the bush.

If a movement of fly towards the rivers is chiefly responsible for the February–March rises in fly-catches each year a more marked rise in catches might be expected each year along riverine patrols during August and September when the non-riverine bush is again dry and leafless. There is the difference, however, that during August the maximum and minimum temperatures are at or near their lowest. Also sunlight and radiation at this time is not so high as during January–February since in August and September the days are generally hazy and cloudy while during February the sunlight is intense with minimum cloud. Although leaf-shade conditions generally are unfavourable for *G. pallidipes* throughout the thicket areas during August and September, the high temperatures and bright sunlight are not present to force the tsetse to congregate near the riverine areas.

Whatever may be the reason, the rise in population along patrol routes near the Keite and Thwake rivers was never so great or so regular in the August–September dry season as in the January–February dry season.

The one great exception to this was during June, July and August 1949 when phenomenal rises in population occurred along most patrols both within and without the settled area.

Once again we must postulate in terms of fly movements and it was suggested that the abundance of fly in the western settled area (fig. 5) was due to movement of fly upstream. For instance, the rise was first noticed in patrols nos. 28 and 30 at Kikumeni camp in June and July 1949, while upstream in the settled areas around Woti camp and further west the peak rises were in August, September and October. There was, however, no decrease in fly around Kikumeni during August and September to correspond to the suggested mass movement of flies going westwards, and altogether the evidence for movement of fly upstream on a grand scale at least from the Kikumeni area is not very convincing.

In the settled area the increase in catches was first noticed suddenly on the 13th and 14th of July when flies were caught in considerable numbers along roads and paths. When flies continued to increase additional labourers were employed to catch out this invading population and the result of their efforts are shown in fig. 17. The peak catches were in October, and on the 6th October 269 flies were caught by the labour gang in addition to those caught by regular patrols as shown in fig. 5.

That these flies were invading the area may be deduced from the appearance of this curve since they appeared suddenly, and decreased rapidly towards the end of October. Also the majority of flies caught were old flies, the number of females caught was usually over 50 per cent. of the total caught and 75 per cent. of the males caught were hungry flies. There was a distinct tendency for flies to increase first along definite riverine patrols such as patrols nos. 8, 9, 10, 11 and 12 and later along patrols further away from the river such as patrols nos. 13, 14, 15 and 16. In any case, no increased breeding was ever discovered in the settled area or elsewhere at this time.

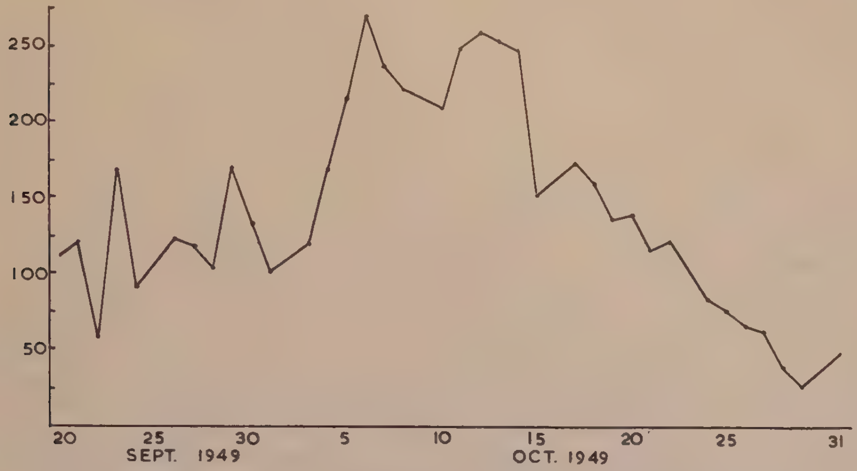


Fig. 17.—Total number of *G. pallidipes* caught on each of 36 separate catches by 20 untrained labourers in the settled area during September–October 1949.

The origin of the flies which appeared in the settled area will always be a matter of some doubt. Although the rise in catches at the Kikumeni camp were earlier than those of the settled areas it has already been stated that there is no evidence to show that flies then left this area and moved upstream. The evidence around the Thwake camp is different since the increase never really developed here to any marked extent (figs. 6 & 7). It is possible therefore that flies moved westwards from Thwake into the settled areas. In addition, flies could easily move inwards into the settled areas from a north or south direction, especially from the north.

The reasons for this abnormal movement can also only be guessed. The year 1949 had an unusual rainfall pattern. Most of the rainfall in the settled area fell in April (fig. 4). The total rainfall at Woti camp on the eastern edge of the settled area during May to September for the years 1949, 1950 and 1951 was 0·77, 1·68 and 5·34 inches respectively. The rainfall at the more eastern camps was not recorded but is always less. The maximum temperatures during September and October 1949 at Woti were also higher than usual (fig. 2). In accordance with the low rainfall and high temperatures it was noted that vegetation was more leafless during August 1949 along the Thwake river at Thwake than along the Keite river in the settled areas. Also we have already noted that vegetation on the higher ground around Unoa Hill and in the settled areas contains less *Commiphora* spp., and more *Combretum* and *Dalbergia* spp., than that around the eastern Thwake and Kikumeni camps, and this provides more dry season shade. The riverine vegetation around Thwake camp was being cleared early in 1949 and so shade in this area was still further reduced.

It might be suggested therefore that owing to climatic conditions the tendency for flies to leave the *Commiphora* bushland and seek riverine shelter during July, August and September 1949 was greater than usual. Flies moving in towards the river around the Kikumeni camp found conditions tolerable and numbers continued to increase in this area from June to November 1949 (figs. 8 & 9). Flies moving in to the river around Thwake camp found conditions less tolerable and dispersed elsewhere especially during the hotter months of September and October. Those moving westwards into the settled areas where shade was more near the optimum than in any of the other areas were detected at once and the invasion recognised.

While agreeing with Nash (1930, 1933) and Jackson (1944) that catches of flies on regular rounds afford a reliable measure of changes in true density, the activity of the flies may also have increased at this time in the relatively cleared and settled areas. They tended to congregate more than usual along roads and paths where visibility was good and opportunity to obtain a blood meal was more hopeful. Under these conditions they came more readily to screens carried by fly-boys and catches were further increased.

The effects of rainfall on the distribution of *G. pallidipes* along the main rivers at Thwake can be further deduced by comparing the catches during May to December 1950 with those over the same period during 1951. The abnormally high rainfall during 1951 corresponded with decreased catches along patrols from Thwake (figs. 6 & 7) as compared with 1950 when rainfall was more normal. The decreased catches at Thwake in 1951 did not, however, produce any invasion of the settled areas and it appears safe to assume that it reflected a greater tendency for flies to remain in the open bushland where the continued rainfall had produced more shade than usual.

Conditions however at Kikumeni, where the bushland is drier and the proportion of *Commiphora* spp. greater than at Thwake, produced a riverine migration even in a wet year (figs. 8 & 9).

If these postulations hold good one may predict an invasion of the western areas during a year when the rainfall for the May to September period is less than 1 inch, as low rainfall usually corresponds with low cloud density and increased radiation and maximum temperature.

Summary.

The Makueni fly belt is chiefly infested with *Glossina pallidipes* Aust. and lies between 4,000 and 2,600 feet above sea level. The climate is hot and dry with two wet and two dry seasons, annually. The dry period during January and February is hot with bright sunlight while during the June to September dry period the temperatures are lower and with dull cloudy periods. The vegetation is *Acacia-Commiphora* dry grassland association with the *Commiphora* especially predominating at the lower altitudes in the east. The non-riverine deciduous bushland and thickets show two leafless periods in the year, corresponding with the dry seasons. A system of regular fly patrols has been in operation in this area since January 1949. The total flies caught show a regular seasonal increase during February–March each year and less regular and smaller increases during June–July and October–November. The same seasonal increases in the fly-populations are shown by the average number of old male flies caught per patrol.

Flies caught during 1951 were fewer than in 1950 in the settled areas and at Thwake camp, but at Kikumeni in the dense *Commiphora-Acacia* thickets the catches in 1951 were at least as numerous as in 1950.

Teneral flies formed a greater proportion of flies caught at Thwake camp than at Kikumeni. There was, however, no rise in the number of tenerals caught to correspond with the seasonal increases of total flies caught.

The percentage of male flies in catches was higher at Thwake camp than at Kikumeni.

It is suggested that the February–March rise in flies caught is due to a movement of flies inward from the dry bushland to the cooler more shady riverine areas. At Thabu this movement from *Commiphora* orchard country to shady riverine areas during February 1952 is shown by comparison of the returns from two patrols sited respectively in these two habitats.

The movement of fly towards riverine shade is not so marked during the long dry months of July, August and September because the weather is cooler and radiation less intense.

The fly "invasion" experienced during the June–October period of 1949 coincided with an abnormally dry hot season and fly moved in abnormal numbers not only inwards to the riverine shade but westwards towards the increased shade to be found in the *Combretum-Dalbergia* association in the settled areas. There may also have been increased activity of *G. pallidipes* at this time.

The effects of rainfall and humidity on the distribution of a *G. pallidipes* population is also seen when the total flies caught at Thwake camp during 1950 are compared with those caught during 1951.

Acknowledgements.

My acknowledgements are due to our Field Staff, both European and African, who daily traversed the rhino-infested bush to collect the data on which this paper is based.

The paper is published with the kind permission of the Director of Veterinary Services, Kenya.

References.

Jackson, C. H. N. (1944). Ann. Eugen., **12**, pp. 176–205.

Moggridge, J. Y. (1936). Bull. ent. Res., **27**, pp. 449–466.

Nash, T. A. M. (1930). *Ibid.*, **21**, pp. 201–256.

Nash, T. A. M. (1933). *Ibid.*, **24**, pp. 107–157, 163–195.

Parsons, B. T. *Ibid.*, **45**, pp. 163–174.

Wilson, S. G. (1952). Trans. 9th int. Congr. Ent., **1**, pp. 971–976.

FIELD OBSERVATIONS ON A BREEDING PLACE OF *GLOSSINA PALLIDIPES* AUSTEN IN KENYA.

By B. T. Parsons, M.A.

Field Zoologist, Kenya Tsetse Survey and Control.

Routine searches for puparia of *G. pallidipes* Aust. were made between April 1949 and June 1952 in a limited area, in the eastern part of Machakos District, Kenya, where conditions are specially favourable for the breeding of this species. The aim was to discover something of the biology of this versatile and adaptable species of tsetse in one of its main "strongholds"—the semi-desert thorn country which occupies vast stretches of Kenya and adjacent territories. *G. brevipalpis* Newst. was also present, but in much smaller numbers, and data on this fly are omitted throughout.

General Description of the Breeding Site.

The area studied was on the banks of the Kiangine river, a typical seasonal tributary of the Athi river drainage system. The altitude was 2,800 ft., and the river had steep banks, a winding course, and a dry sandy bed except for a few weeks in the year when the rains fell and turned it into a muddy torrent. For most of the year there was a sharp contrast between a narrow 5 to 50 yard zone of evergreen trees and shrubs on the river banks and the thorn scrub of the surrounding country. The latter contains *Commiphora* spp., acacias, baobab (*Adansonia digitata*) and associated shrubs, and has been described by Wilson (1954). The evergreen vegetation varied far less in seasonal appearance than the vegetation of the surrounding country.

The breeding-place studied was inside the evergreen shrubs, chiefly *Craibia* sp. with a few large *Cordia* sp., and with a scattered tree canopy of species of *Acacia*, *Mimusops* and *Piptadenia*. Herbage was practically absent, and it was possible to walk about under the shrubs, an exceptional feature in a *pallidipes* breeding-place. The soil was sandy, with a good deal of dark humus-containing material and dead-leaf cover constantly renewed from the *Craibia*, which acquires new leaves in November–December and sheds old ones throughout the year.

Methods of Search for Puparia.

The main object was to carry out a regular monthly search under supervision in a chosen area. In April 1949, a rectangle of 20 × 10 yards (200 sq. yd.) was marked out with small posts at 2-yard intervals, and this was called "Breeding-Site A". At the same time, a fly-patrol route of approx. 3½ miles was selected, going through country adjacent to the breeding-site on both banks of the river. Searches were made by teams of African fly-boys, usually 7 to 10 in number, and efforts were made to remove all full and empty puparia.

The practice was to start at one end of the site and work systematically to the other, preserving the leaf-cover as far as possible, and spreading it out after the search. In the next search a start was made from the opposite end, so that the soil was not all moved away in one direction. Generally, by the time the next search took place, the ground did not appear much disturbed, neither did it look greatly different from nearby unsearched portions. Searching was done by hand, a pointed stick being used to dig and crumble the soil only when it was damp (about four months in the year). The efficiency of hand-searching was tested by marked samples of *pallidipes* puparia.

Data were thus collected on the seasonal variation in numbers of puparia, and on the fly-numbers in the patrol. In a good many cases some information was obtained on parasitisation of pupae. Observations on vegetation changes were also made, and meteorological data collected (see below). Later the breeding-site shrubs were charted and the position of each full puparium plotted in relation to the distribution of the *Craibia* shrubs. This part of the work was started in February 1950, when a second site, known as " B ", also of 200 sq. yd., was chosen on the river bank about 600 yards upstream from " A ". Vegetation in " B " was also charted, and it was searched monthly; but the full puparia were replaced after being marked with coloured paint. Data were collected on the hatching-success from these puparia and on their duration in the site under completely natural conditions.

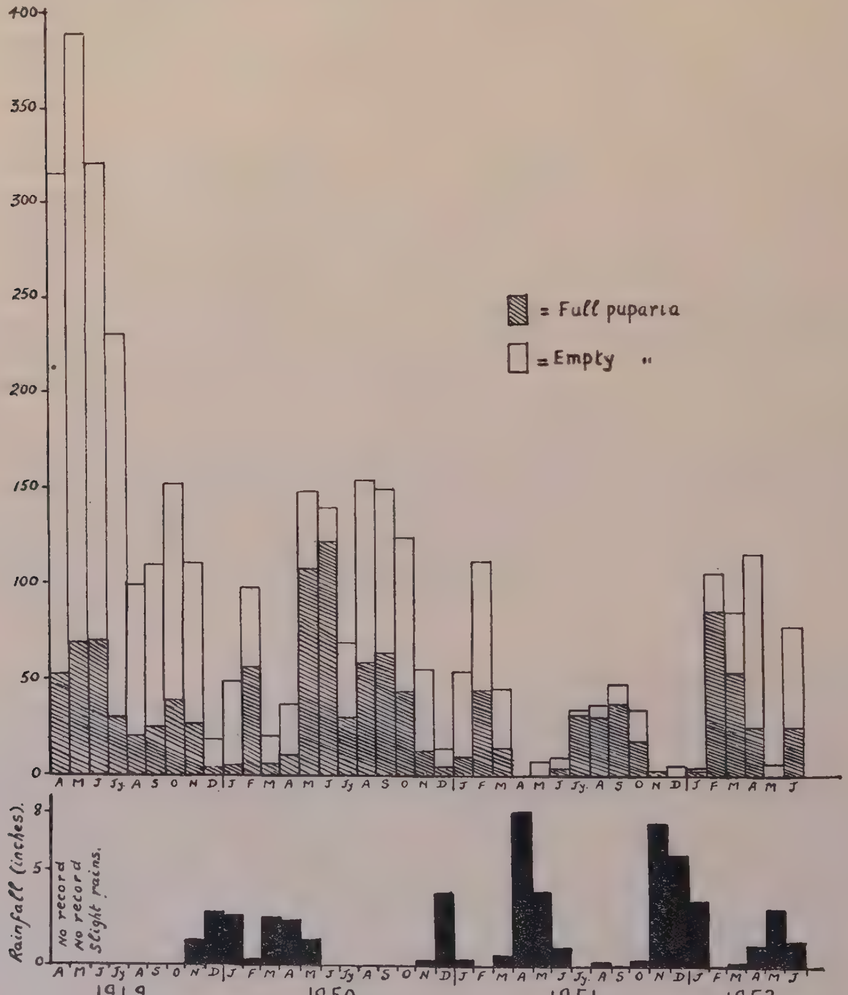


Fig. 1.—Numbers of full and empty puparia of *G. pallidipes*, and rainfall in breeding-site " A ".

Finally, in June 1950, a third site, also of 200 sq. yd., known as " C ", was marked out in a rather denser piece of shrubbery, with several very large *Cordia* sp., close to " A ". This last place was searched every three months and all full and empty puparia removed, to see whether there was any significant difference between it and a site disturbed each month.

None of the sites was enclosed, and all were subjected to treading and scratching by the varied and numerous fauna of mammals and birds found in this wild country.

Meteorological Data and Climate.

A small strongly-built grass hut close to one end of site " A " was fitted in June 1949 with maximum, minimum, wet- and dry-bulb thermometers five feet from the ground, and with a thermometer buried one inch below the surface of the soil. Daily readings were taken, in the early morning and at 2 p.m., the instruments and readings being checked by a supervisor whenever possible. A rain-gauge was kept in the camp, about $\frac{3}{4}$ mile distant, and read at 8.30 a.m. daily. Another rain-gauge was operated for a time close to the hut, under the shrubs; but it was swept away by the floods in April 1951.

The climate of this type of country is severe, with periods of intense heat and low humidity, sudden torrential rain, and two well-marked dry and two wet seasons annually. It has been described by Wilson (1954). The effect of such a climate on the vegetation outside the narrow evergreen riverine belt is to cause most of its component trees to leaf twice a year (October–November and again in March–April), and to make many plants appear grey and leafless for nine months out of the twelve.

Results from Breeding-Site " A ".

The monthly figures for puparia collected, the average catches of *pallidipes* on the fly-patrol, and the meteorological data are given in Table I. With regard to the latter, these have been worked out for the month ending on the date of the search for puparia, which was usually made about the 14th of the calendar

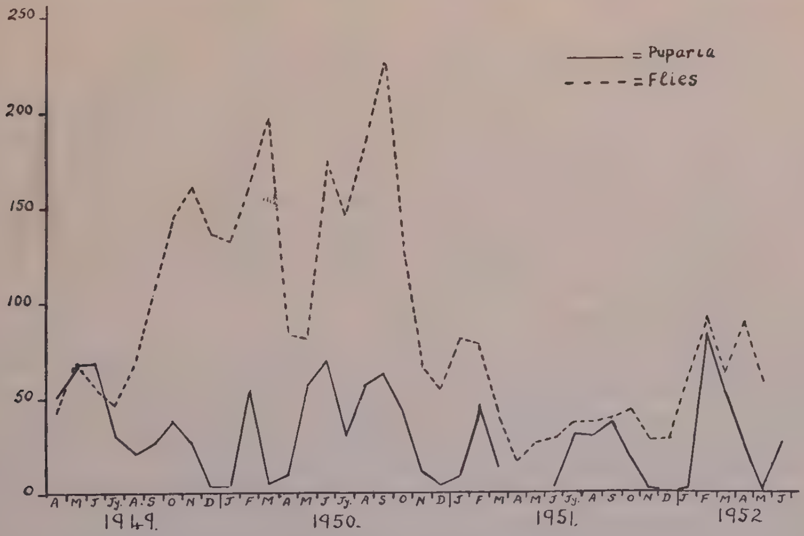


Fig. 2.—Numbers of full puparia of *G. pallidipes* and average numbers of flies taken monthly by fly-patrol in breeding-site " A ".

month. The numbers of full and empty puparia are shown against rainfall for the month in fig. 1. Numbers of full puparia only, against fly-patrol averages, are shown in fig. 2.

TABLE I.

Numbers of full and empty puparia recovered at breeding-site " A " with numbers of flies caught on patrol, and meteorological data.

Month	Full puparia	Empty puparia	Patrol average no. of flies	Rain in in.	Average temperatures in °C.		
					Max.	Min.	Ground
Apr. 1949	52	265	41	c.3	No Record		
May	68	321	69	c.5	„	„	
June	69	251	57	Nil	„	„	
July	30	200	47	Nil	29·4	14·5	23·4
Aug.	22	77	69	Nil	28·1	(17·2)	23·5
Sept.	26	83	105	Nil	29·7	16·3	23·9
Oct.	38	114	145	Nil	31·5	15·8	24·9
Nov.	27	83	161	1·37	33·6	16·8	25·1
Dec.	3	15	137	2·84	33	15·7	23·7
Jan. 1950	3	46	132	2·63	31·7	16·4	24
Feb.	56	40	161	0·27	33·9	16·2	24·4
Mar.	5	15	199	2·63	34·4	16·8	25·2
Apr.	10	27	84	2·44	31·1	18	24·4
May	108	39	81	1·36	30	17·2	23·8
June	122	16	175	Nil	29·6	13·5	23·5
July	30	39	145	Nil	28·4	13·8	23·3
Aug.	58	94	184	Nil	26·5	12·3	22·1
Sept.	64	84	227	Nil	29·3	12·8	23·7
Oct.	43	79	129	Nil	29·3	15·8	24·3
Nov.	12	43	66	0·30	32·2	17·4	25·4
Dec.	3	10	55	3·86	31·6	(19·2)	24·5
Jan. 1951	8	45	82	0·36	31·3	15·9	24·1
Feb.	44	68	80	0·06	32·8	15·4	25·3
Mar.	13	32	42	0·59	33	17·6	26·1
Apr.	No search		16	8·15	29·1	19·6	24·3
May	Nil	7	25	3·81	27·9	17·7	22·7
June	3	5	29	0·97	27·4	18	22·3
July	31	3	37	Nil	27·4	14·2	21·7
Aug.	30	7	37	0·09	27·2	14·1	21·9
Sept.	37	10	38	Nil	28·8	15·4	23·7
Oct.	18	16	44	0·17	30·5	16·7	25·9
Nov.	1	Nil	28	7·54	29·6	19·4	23·7
Dec.	Nil	5	28	5·77	28·1	18·8	23·3
Jan. 1952	1	2	61	3·44	28·4	20·1	23·2
Feb.	85	20	94	Nil	28·8	18·5	24
Mar.	53	32	63	0·09	29·9	18·1	25·7
Apr.	25	89	90	1·10	33	19·3	25
May	Nil	7	59	3·13	34·2	19·9	24·8
June	26	51	—	1·28	30·4	19·1	24·5

Some interesting facts emerge from the above Table and from the graphs. Particularly noticeable is the continuous use of the breeding-site by *pallidipes*, despite monthly disturbance of the ground; only on 3 out of 38 occasions were no full puparia discovered. The numbers of puparia per 200 sq. yd. fluctuate widely, and there is a tendency for three peak periods during the year. Of these the February rise is most marked and coincides with severe heat and dry conditions. Another peak in April and May was noted in 1950, while there is a tendency for numbers to increase again in September and October, at a time when no rain has fallen for several months and the non-riverine bush is extremely dry. The low numbers of full and empty puparia found during wet months are partly due to the greater difficulty of seeing such objects in damp soil; but the rise in numbers of full puparia in February is very striking. The year 1951 was remarkable for flooding, owing to a very heavy spate in the river early in April. A note on the effect of floods is included later, and it suffices now to say that the pattern of breeding has been much the same since the floods, though in somewhat smaller numbers.

The huge accumulation of empty puparia took some months to remove; and it was not until the 11th search that "fulls" exceeded "empties". In the hot period of January to March a higher proportion of "empties" would be expected owing to more rapid hatching, but this does not seem to be borne out by the figures. On the other hand, there appears to be a greatly accelerated rate of larviposition in the site between the January and February searches.

With regard to the fly-patrol figures, it is only in the latter part of the time that any close correspondence can be seen between numbers of full puparia and the average fly-catch. It should be borne in mind that there are huge stretches of an alternative type of breeding-ground available during the rainy seasons, and that even in laboratory conditions *G. pallidipes* can live up to four months, so

TABLE II.

Numbers of *G. pallidipes* puparia found parasitised on rearing under laboratory conditions.

Month	Puparia	Puparia which produced *pallidipes* (1)	Puparia which produced parasites (2)	(2) as % of (1 + 2)	Notes
Apr. 1949 ..	52	22	12	35	Sent to Kabete
May ..	68	23	27	54	,,
June ..	69	42	15	26	,,
July ..	30	5 (3 ♂♂ 2 ♀♀)	8	61	,,
Aug. ..	22	2 (1 ♂ 1 ♀)	4	66	,,
Sept. ..	26	11 (4 ♂♂ 7 ♀♀)	2	15	,,
Oct. ..	38	14 (8 ♂♂ 6 ♀♀)	1	6·6	,,
Nov. ..	27	7 (1 ♂ 6 ♀♀)	2	22	,,
Feb. 1950 ..	56	33 (17 ♂♂ 16 ♀♀)	5	13	,,
Mar. ..	5	3 (2 ♂♂ 1 ♀)	2	40	,,
Apr. ..	10	5 (4 ♂♂ 1 ♀)	3	37	,,
July ..	30	12 (3 ♂♂ 9 ♀♀)	9	43	,,
Aug. ..	58	14 (7 ♂♂ 7 ♀♀)	15	51	,,
Sept. ..	64	41 (14 ♂♂ 27 ♀♀)	2	5	,,
Oct. ..	43	22 (10 ♂♂ 12 ♀♀)	5	18	,,
Nov. ..	12	5 (2 ♂♂ 3 ♀♀)	Nil	Nil	,,
Jan. 1951 ..	8	2 (2 ♀♀)	5	71	Kept at Makueni
Feb. ..	44	17	13	45	,,
Mar. ..	13	2 (2 ♀♀)	7	77	Sent to Kabete
July ..	31	2 (1 ♂ 1 ♀)	2	50	,,
Aug. ..	30	14	12	46	Kept at Makueni
Sept. ..	37	19 (10 ♂♂ 9 ♀♀)	1	5	,,
Oct. ..	18	9 (5 ♂♂ 4 ♀♀)	3	25	,,
Feb. 1952 ..	85	45 (21 ♂♂ 24 ♀♀)	23	34	,,
Mar. ..	53	35 (19 ♂♂ 16 ♀♀)	9	20·5	,,
Apr. ..	25	14 (8 ♂♂ 6 ♀♀)	3	21	,,

that no very close relation could be expected between the two sets of figures. The flooding of April 1951 did, however, have a very deleterious effect on the local fly-population.

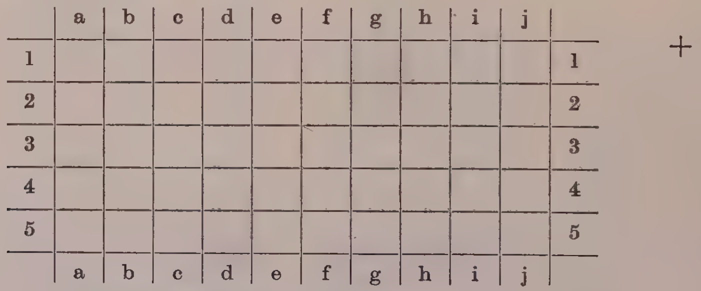
Table I shows that the ground temperature follows the fluctuations of the maximum temperature fairly closely, with peaks in February and again in October and November; the coolest period was in August. The minimum fluctuates more often, with peaks in November—December and April—May, and periods of low minimum temperature in February and August when skies are often clear and the air cools rapidly after sunset. The three peak periods for full puparia coincide fairly well with times of low minimum temperature.

Table II summarises information about hatching and parasite percentages of some of the collections from breeding-site " A ". Some of the collections were sent to the H.Q. laboratories at Kabete, and others were kept at Makueni, about 25 miles from the breeding-site (alt. 4,000 ft.). There was a good deal of variation in the degree of success in hatching, and the rate of parasitism, chiefly by *Thyridanthrax* sp., fluctuated widely. Of the *pallidipes* whose sexes were recorded, 140 were male and 162 female.

By analysing the vegetation and splitting up the breeding-site into small squares of 2 yards side (see diagram below) it has been possible to determine the parts of the site which were most and least favoured for larviposition. The observations fall into two parts, as the floods of April 1951 swept away topsoil and did much to alter the distribution of the puparia.

The vegetation of breeding-site " A " consisted of 469 *Craibia* sp. (dominant), of which 230 were under 3 ft. high and 23 between 12 and 25 ft. high. Thirty-one *Cordia*, mostly small, and a few plants of *Capparis kirkii*, *Thylachium* and *Phyllanthus* made up the balance of 528 plants.

Between February 1950 and March 1951, " A " was searched 14 times. Squares in which the highest totals of pupae were found and that in which pupae were found most frequently (a5) are detailed below, and the following diagram shows the arrangement of the squares:—



+ Position of hut with meteorological instruments.

Sq. no.	No. pupae	*Craibia* over 6 ft.	*Craibia* 0–6 ft.	Other plants
b1	37	3 (2×20 ft., 1×10 ft.)	5	Large *Cordia* (20 ft.)
a1	34	3 (2×20 ft., 1×7 ft.)	Nil	1 herb (fam. ACANTHACEAE)
a2	33	1 (12 ft.)	4	3 herbs
a5	Greatest frequency pupae found 11 searches out of 14	1 (8 ft.)	7	*Phyllanthus*, *Commelina*, herbs

Thus, in each of the four squares, a two-storeyed vegetation of *Craibia* was present, together with a top-canopy of nearby *Acacia* and *Mimusops* trees. Three squares in site " A " only produced one full puparium during the period under review.

The floods of April 1951 did not carry away the *Craibia* shrubs, though some of them were bent down. The leaf-cover and topsoil were scoured away, and much river-sand or muddy silt left in their place. No search was possible in April, while in May digging the still damp soil only yielded a few old empty puparia. In June, however, three full puparia were found in site " A ", and by July flies were depositing larvae in fair numbers—a feature being the concentration of full puparia under masses of twigs and débris left by the river. Often they could be found lying on firm soil under débris as much as six inches thick.

The leaf-cover slowly returned; but the deposits of coarse sand rendered many of the squares unproductive. Details of the findings during the period after the floods from June 1951 to May 1952 are as follows:—

Sq. no.	No. of pupae	*Craibia* over 6 ft.	*Craibia* 0–6 ft.	Other plants
e5	25	1 (10 ft.)	4	Nil
b1	22	3 (2×20 ft., 1×10 ft.)	5	Large *Cordia*
c5	21	2 (1×14 ft., 1×7 ft.)	Nil	Small *Cordia*
f5	Greatest frequency pupae found 8 searches out of 12	3 (2×14 ft., 1×7 ft.)	23	Nil

All these squares again have a two-storey vegetation. On one occasion 11 pupae were found in e5 in about one square yard under a heap of flood débris.

At several of the monthly searches 20 *pallidipes* puparia, after having been so treated as to kill the pupae and prevent hatching, were marked with a small dot of paint, and hidden in site " A " on the same day, but before the fly-boys came to do their work. However, the men could not avoid knowing that there were marked puparia there, otherwise these puparia would have been included in the monthly chart. On no occasion were all 20 recovered at once, so that a further complication was introduced by the discovery of marked puparia from previous tests. The numbers of puparia found by the boys ranged from 5 to 12 out of 20, and the average efficiency was 37 per cent. The best performance was in a dry-season search. The balance of puparia left over and present at the next search could not be determined, but some were recovered up to three months after being hidden. It is realised from the above that all results are purely relative, and that no claim can be made as to the actual numbers of puparia.

Results from Breeding-Site " B ".

From June 1950 onwards all full puparia were marked with a dot of paint and replaced, each with a small stick marking its position which was charted. At subsequent searches those puparia found empty were removed, and those still full were replaced to await next month's search. The proportion of recoveries was very high on the whole, and the sticks little disturbed despite the almost daily passage of baboons through the site.

Table III is an analysis of the results of these searches.

At the end of the first month the percentage of marked puparia found empty varied greatly, but was never much below 40 per cent. of those recovered. Hatching time depends not only on soil temperature but also on the presence or absence of parasites (a delaying factor when present). In practice it was not possible to tell whether a hatched puparium had contained a tsetse-fly or a parasite.

TABLE III.

Results of monthly searches of breeding-site " B " showing full and empty puparia recovered.

Month	Full marked puparia replaced	Recovered after 1 month		Empties removed in subsequent months				Total empties recovered
		Full	Empty	2nd	3rd	4th	5th	
June 1950	38	14	10	6	4	1	—	21 (55%)
July ..	25	5	6	3	1	4	2	16 (64%)
Aug. ..	27	14	8	8	—	—	3	19 (70%)
Sept. ..	21	8	6	7	—	1	—	14 (66%)
Oct. ..	29	3	13	1	—	3	—	17 (58%)
Nov. ..	24	9	7	4	3	2	—	16 (66%)
Dec. ..	1	1	—	—	1	—	—	1 (100%)
Jan. 1951	7	4	3	1	Floods	—	—	4 (57%)
Feb. ..	14	2	8	Floods	—	—	—	8 (57%)
Mar. ..	8	No search		—	—	—	—	—
July ..	12	7	5	5	1	—	—	11 (91%)
Aug. ..	14	3	9	3	—	—	—	12 (85%)
Sept. ..	9	3	6	2	—	—	1	9 (100%)
Oct. ..	50	8	12	—	1	4	8	25 (50%)
Jan. 1952	1	1	—	1	—	—	—	1 (100%)
Feb. ..	43	15	24	11	—	—	—	35 (81%)
Mar. ..	23	3	18	—	—	—	—	18 (78%)

At the end of the second month in nearly all cases a further substantial group of empties could be removed, lending support to the idea that flies hatch in from four to five weeks under these conditions; and that the most recently-laid ones marked at any search will have hatched between the first and second subsequent searches.

Data from collections of puparia from breeding-site " A " and from a few puparia obtained from captive *pallidipes* flies at Unoa Hill, Makueni (alt. 4,000 ft.) show that most of the flies from a " wild " collection hatch in the first five weeks (av. max. temperature 83°F.); and that parasites may continue to hatch up to the eighth or ninth week. Puparia obtained under laboratory conditions hatched in from 36 to 46 days with the average maximum temperature of 77–79°F.—somewhat cooler than at the breeding-site.

Similar observations to those in site " A " were also made on the relation of these puparia to vegetation distribution. The most striking phenomenon was in October 1951, when, out of 50 full puparia 39 were found concentrated in a shady area under a group of large *Craibia*, occupying only about 6 sq. yards in the centre of the breeding-site.

Results from Breeding-Site " C ".

This site was first marked out in June 1950, being about 60 yards upstream from " A " and of the same size. The vegetation was very similar, but contained several large *Cordia* which gave a dense shade and provided an abundant supply of dead leaves. Probably for this reason, " C " has always yielded more *G. brevipalpis* puparia than either " A " or " B ". Altogether eight complete searches were made at quarterly intervals, the June and September searches being during the early and late dry season, respectively, while the March search was just before the long rains and the December search during the short rains.

As with " A " the first searches removed a great quantity of empty puparia.

The results of searches in " A " and " B " (both disturbed monthly), and " C " (disturbed quarterly), from June 1950 to March 1952, inclusive, are shown in Table IV. " C " was also swept by floods with the same general effect as in the other two sites, and much of the dark humus-containing sand was removed. Nothing was done to " C " after flooding until June 1951, nearly 2½ months after the floods had subsided.

TABLE IV.

Number of full and empty puparia in the three breeding-sites.

Month	Number of full puparia			Number of empty puparia		
	'A'	'B'	'C'	'A'	'B'	'C'
June 1950	122	38	155	16	86	340
July ..	30	25	—	39	50	—
Aug. ..	58	27	—	94	85	—
Sept. ..	64	21	66	84	64	443
Oct. ..	43	29	—	79	38	—
Nov. ..	12	24	—	43	66	—
Dec. ..	3	1	7	10	10	53
Jan. 1951	8	7	—	45	17	—
Feb. ..	44	14	—	68	35	—
March ..	13	8	34	32	33	333
June* ..	3	Nil	4	5	Nil	48
July ..	31	12	—	3	5	—
Aug. ..	30	14	—	7	—	—
Sept. ..	37	9	73	10	16	52
Oct. ..	18	50	—	16	17	—
Nov. ..	1	Nil	—	Nil	2	—
Dec. ..	Nil	No search	2	5	—	4
Jan. 1952	1	1	—	2	4	—
Feb. ..	85	43	—	20	8	—
Mar. ..	53	23	46	32	17	96

* First search after floods during April–May 1951.

A comparison between the numbers of full puparia for corresponding months in " A " and " C " shows a similar trend. In the last of the eight searches the total of 46 puparia for " C " is below the total of 53 puparia for " A ". The searches during March 1951 and September 1951 gave a much higher result for " C " than for " A ". It would be expected that totals for " C " would be higher in all cases if puparia take more than one month to hatch.

The numbers of empties in " C " were much higher than in the other two breeding-sites up to the time of the floods, presumably due to the accumulation of years. After flooding, the numbers remain higher, even when one compares the " C " total with the 3-months' total for " A " and " B ". The general conclusion is that more frequent disturbance has not had an unfavourable effect on the original breeding-site at " A "; and that floods have not seriously interfered with breeding.

Site " B " has usually been less productive than " A " and only during November 1950 and October 1951 were more full puparia found in " B " than in " A ". Otherwise the fluctuations in numbers have been fairly comparable.

Discussion of Results.

All three breeding-sites, but particularly " A ", were in almost continuous use by *G. pallidipes* throughout the year. This is to be expected if it is realised that the riverine vegetation provides a far more uniform environment throughout the year than the other vegetation types. Being always in leaf, it contrasts sharply with the leafless, grey, thorn-scrub away from the rivers during the dry seasons.

On the other hand, the numbers of full puparia found at monthly intervals have shown very wide fluctuations. The reason for this is not fully understood, but there is no doubt that several very different factors are at work.

Reference to Table I and fig. 1 shows that the rainfall, which has a marked effect on non-riverine vegetation (Wilson, 1954) in these dry scrub areas, coincides with a period of reduced use of the evergreen sites. On the other hand, neither the maximum nor the soil temperatures appear closely related to the numbers of full puparia. The minimum temperature fluctuates considerably and the peak periods for full puparia tend to coincide with times of low minimum temperature.

It is suggested that, during rainy periods, vast stretches of an alternative type of breeding-place are freely used by *G. pallidipes*, but at a much lower density. As the non-riverine vegetation loses its leaves with the advance of the dry seasons, so there will be a movement of flies back towards the riverine vegetation with increased use of these areas for breeding. Some confirmation of this from the point of view of adult flies is already given in Wilson's paper (1954); and the results from Thabu Camp relate to country very similar to that at Kiangine, the Chunyu river in patrol 49 being a tributary of the Kiangine.

The reason for relation between low minimum temperature and peak breeding is possibly that at these times the night skies are clear, and there is increased heat-loss from a bare soil and leafless bush, which will be recorded even in the meteorological station. Thus the low minimum is another indication of the state of the non-riverine deciduous trees and thickets. The apparently abnormal numbers of puparia found in June 1950 was at a time of very low minimum temperature.

A preliminary study of the main non-riverine type of breeding-place was made in 1951, from May to September inclusive. The thickets consisted chiefly of *Combretum exalatum*—a shrub up to 10 ft. high, which is in leaf from November to July, but during much of the dry season has the leaves in a rolled-up and wilted condition. Various trees, such as *Lannea* sp., *Delonix elata* and *Commiphora* sp., formed a top canopy, while the shrubs had an undergrowth of *Sansevieria robusta.* The soil was reddish, up to 6 in. deep and contained much dead plant remains. The thicket examined was about 100 yards from the bank of the river. In practice only a small area was searched each month, and it was not possible to subject it to regular monthly treatment as was given to sites " A ", " B " and " C ". In order to search for puparia at all it was necessary to root out all the *Sansevieria*, thus altering the nature of the breeding-site. Only 40 sq. yards were searched each month, and either full or empty puparia of *G. pallidipes*, *G. brevipalpis* and *G. longipennis* Corti were all found. The numbers of *G. pallidipes* puparia were 29 empties in May, 2 full and 179 empties in June, 97 empties in July, 77 empties in August and 1 full and 134 empties in September.

A great deal of widespread searching and further study is required in this type of site, probably in the form of small samples chosen over a wide area, as the thickets extend up to three miles from the river. It is enough now to say that such places undoubtedly have an important rôle in the ecology of *G. pallidipes*.

A further reason for decrease in the numbers of puparia found in the wet-season searches may be in the increased numbers of predatory animals such as ants, scorpions, centipedes, which were often encountered in the damp soil. The poor recovery in site " B " in November 1951 after marking 50 puparia in October 1951 may have been partly due to this factor.

Very large numbers of full puparia have been collected from riverine breeding-places on the Kiangine river at different times, and it can be seen that with 100 puparia in site " A ", the density per acre will be over 2,000, or over 1,200,000 puparia per square mile.

The results from the fly-round, which was patrolled by two boys with a blackened " screen ", 6 ft. × 3 ft. as in other Makueni patrols, were not very striking, but they did show the high catches in February (particularly 1950) and September (especially 1951), with a decrease in April and November noted elsewhere in Makueni (Wilson, 1954, pp. 148–150).

Breeding-site " B " figures for full puparia confirmed in general those from " A ". The rise in February 1951 was a good deal less marked; but that in October 1951 was very striking; and the concentration of the latter puparia in relation to shade has already been noted. On the whole, the numbers of marked puparia recovered were very much larger than expected, and their persistence in the unenclosed site was remarkable. In one instance a *G. brevipalpis* puparium was recovered and replaced for seven consecutive months.

The numbers of full puparia in site " C " also followed the same general trends, but were much higher at the first search after flooding—in June 1951. Empties were nearly always higher than the sum of the preceding 3 months' empties from site " A ". The soil in " C " was deeper and darker in colour than in the other sites, besides which it had been searched less often, so that there had not been the same chance to remove the deeper-lying empties.

The floods seem to have had a depressing effect on the fly-population for at least six months, probably because large numbers of full puparia were swept away and because many larvae were deposited in unsuitable sites when the flies returned to the riverine breeding-places. This return probably took place about two months after the floods. The existence of alternative breeding-places, provided by the *Combretum* thickets already mentioned, probably prevented a more violent decrease in numbers, and these at their lowest were nearly as high as the maximum for other areas of Makueni (Wilson, 1954).

The concentration of puparia under débris was an interesting phenomenon. On one occasion, near site " B " in July 1951, 43 puparia were found in an area of about 12 sq. ft., and later a further 19 were found after the débris had been replaced and left for some days. The situation of some of the puparia was such that larvae must have burrowed down several inches until stopped by firm damp soil below the débris.

Despite all the hours spent on the search for puparia, it was the exception to see a *pallidipes* fly in the breeding-sites; an occasional teneral was sometimes caught, but gravid females were not seen. Most of the work was done between 8.30 a.m. and 4 p.m.

Summary.

A breeding-place of *Glossina pallidipes* Aust., in evergreen shrubs of *Craibia* sp. on the Kiangine river, Makueni, Kenya, was studied by means of hand-searching for puparia in conjunction with records of rainfall and temperature. A fly-patrol was also operated. The country away from the river was thorn-scrub, with *Acacia* and *Commiphora* trees predominating.

Three sites, each of 200 sq. yards, divided into 50 squares, were marked out, and two of them were searched monthly and the third quarterly.

Site " A " was searched nearly every month between April 1949 and June 1952, and full puparia were nearly always found. Numbers varied very widely; and it was noted that few could be found in rainy seasons during the months of November to January and April to May, though 1950 was an abnormal year. A consistently large increase in numbers was observed in February, the hottest and driest month, and a rather less marked increase towards the end of the

long dry season in September and October. Large numbers of full puparia also tended to coincide with times of low average minimum temperature.

The numbers of flies caught on the fly-patrol did not appear to bear any close relation to the numbers of full puparia discovered.

Testing for efficiency of searching by means of marked puparia showed that about 40 per cent. of puparia were recovered, so that results must be taken as relative.

Collections which were kept for hatching showed a widely varying parasite percentage (*Thyridanthrax* sp.), a sex-ratio of approximate equality, and a hatching-time for *G. pallidipes* of 35 to 40 days.

Vegetation analysis showed that squares most favoured for larviposition contained a two-storeyed structure of *Craibia* shrubs.

Site " B " was searched monthly between February 1950 and June 1952, and the full puparia were marked and replaced. The trend of numbers followed that observed in site " A ", but generally in smaller totals, perhaps due to the more open nature of the site. An interesting case of correlation between shade and situation of puparia was noticed in October 1951. Recoveries of the marked puparia were good; and they confirmed that the time for duration of full puparia in the site was between one and two months.

Site " C " was only searched eight times, at quarterly intervals. Very large numbers of empty puparia were removed at the first searches, but there was no significant difference between the totals of full puparia from this site and from site " A ". It was concluded that the more frequent disturbance of the soil in the latter did not have an unfavourable effect on breeding.

Flooding of the sites in April 1951 caused a decrease in the fly-population; and a concentration of puparia under flood-débris in the following June and July was noted.

It is suggested that the existence of large tracts of *Combretum exalatum* shrubs with *Sansevieria*, as an alternative type of breeding-place for *G. pallidipes*, has a marked effect on the use of the evergreen *Craibia* thickets.

Acknowledgements.

I wish to express my grateful thanks to the Director of Veterinary Services, Kenya, for permission to publish this article, to Dr. S. G. Wilson, Chief Field Zoologist, for direction and to Dr. P. E. Glover for much botanical assistance; and to the Field Assistants and fly-boys who did so much of the ground-work without which the paper could not have been written.

Reference.

Wilson, S. G. (1954). Bull. ent. Res., **45**, pp. 141–161.

FINAL RESULTS OF AN EXPERIMENT ON THE CONTROL OF ONCHOCERCIASIS BY ERADICATION OF THE VECTOR.

By P. C. C. Garnham.
Professor of Medical Protozoology,
London School of Hygiene and Tropical Medicine,
and
J. P. McMahon.
Entomologist, Division of Insect-Borne Diseases, Kenya.

Early in 1946 *Simulium neavei* Roubaud was eradicated from the district of Kodera in Kenya Colony by the application of emulsions of DDT to infested streams (Garnham & McMahon, 1947). The human population at that time was heavily infected with *Onchocerca volvulus*, which was being transmitted solely by *S. neavei.* Skin biopsies in March 1947 revealed microfilaria rates of 37 per cent. in children in the 4–8 years age group and 7 per cent. in the 3–4 years. These provide a base-line for future surveys; eight years after the eradication date, the skin of children of such age groups should show no microfilariae. The adult rate in earlier surveys varied between 70 and 85 per cent.

The continued absence of the vector was confirmed by at least yearly surveys since 1946. The last fly was caught on 23rd March of that year. Large numbers of trained Africans supervised by Europeans were employed in these searches, each of which entailed 30–60 boy-hours of catching. A reward of five shillings for an adult *S. neavei* was offered on several occasions but produced no results. The habitat of the immature forms is now known to be the carapace of freshwater crabs (McMahon, 1951), and 1,200 crabs from the Kodera rivers were examined in 1950 with negative results. These findings strongly suggest that the species has entirely disappeared and has not been re-introduced.

Onchocerciasis surveys were repeated in July 1950 and in June 1953, and our findings are given in Table I.

TABLE I.

Occurrence of microfilariae in humans of different age groups.

	0–3 years	4–8 years	9–12 years	Adults
1950				
Number examined ..	21	103	54	31
Number positive ..	0	6	11	11
Per cent. positive ..	0	5·8	20·4	35·5
1953				
Number examined ..	36	120	7	189
Number positive ..	0	6	2	95
Per cent. positive ..	0	5	28·6	50·3

The estimation of ages in African children over 3 years old is difficult, and it is possible that the six positives recorded in the 4–8 years age group in June 1953 were in reality in older children; it is unlikely that the disease was contracted elsewhere, and in the apparent absence of the vector, we find it hard to believe that the infection could have been transmitted locally after March 1946. A further survey was made in September 1953, when estimation of ages was checked by the dentition and in a group of 129 children between the ages of 0 and 7 years, none showed microfilariae in the skin.

The figures relating to the older age groups in Table I provide a useful guide to the duration of infections with this worm in the human host. They indicate that microfilariae are still being produced after seven years; nevertheless, the figures suggest that about a third of the infections have died out in adults after seven years. Clinically, the disease retrogressed after four years to an even greater extent, 3·3 per cent. of the population showed skin lesions in contrast to 15 per cent. before stoppage of transmission, 0·5 per cent. showed eye changes instead of 9·8 per cent., and 0·5 per cent. showed nodules instead of 4·7 per cent. (the pre-treatment figures are taken from Buckley (1949) and refer to the same population). The disease however still exists, though transmission has ceased, and dramatic effects like those following malaria eradication are absent.

Summary.

1. Disappearance of *Simulium neavei* after DDT-treatment of rivers in Kodera, Kenya, is still manifest after seven years, and the species seems to have been eradicated from the district.

2. Skin microfilaria rates have dropped from something under 7 per cent. to nil in the under 4 years age group; from 37 to 5 per cent. or less in the 4–8 years; and from 70 per cent. to 50 per cent. in adults.

3. The length of life of the adult worm can be at least seven years.

References.

Buckley, J. J. C. (1949). J. Helminth., **23,** pp. 1–24.

Garnham, P. C. C. & McMahon, J. P. (1947). Bull. ent. Res., **37,** pp. 619–628.

McMahon, J. P. (1951). *Ibid.*, **42,** pp. 419–426.

THE PICK-UP OF SPRAY DROPLETS BY FLYING LOCUSTS.

By N. W. Wootten.*
Anti-Locust Research Centre,
and
K. F. Sawyer.
Ministry of Supply.

E.M.V.

(Plates IX and X.)

The aerial curtain spraying method of applying insecticides from aircraft to fully flying swarms of locusts has been described by Gunn, Graham and others (1948) and a theoretical treatment for calculating the expenditure of spray given by Sawyer (1950). The complete solution of the equation derived in the latter treatment required an experimental determination of the values to be assigned to the Horizontal Equivalent Area (see below) and the toxicity of the insecticide solution as a function of spray droplet size. The present paper describes a laboratory investigation of these two variables under conditions approaching as nearly as possible those of natural flight.

Similar measurements made previously by Kennedy, Ainsworth and Toms (1948), were obtained under less ideal experimental conditions using *Locusta migratoria migratorioides* (R. & F.) and various insecticides. The work described here was carried out with *Schistocerca gregaria* (Forsk.), the species giving most concern at the time the work was commenced. The insecticide was dinitro-ortho-cresol (DNC) as 20 per cent. w/w strength in oil, known as Mk. IV solution. This solution has been shown by field trials (Gunn, Lea & others, 1948) to be well suited to aircraft spray operations.

The investigations were divided into three parts. Firstly, the development of a technique to produce "natural" flight under conditions suitable for the later experimental measurements; secondly, a measurement of the Horizontal Equivalent Area as a function of droplet size and locust airspeed; and, thirdly, a determination of the lethal effectiveness of a given quantity of the insecticide solution when applied in droplets of various sizes to flying locusts.

Locust Flight Characteristics.

Experimental requirements.

Before measurements of the Horizontal Equivalent Area and toxicity of the spray could be made it was necessary to ascertain the experimental conditions under which a locust would exhibit the characteristics of natural flight, whilst constrained in a manner which would enable the required measurements to be made. These characteristics include the airspeed, wing beat frequency and amplitude, the body angle with respect to the horizontal and the position of the legs in flight. (See, for example, fig. 22 in Gunn, Perry & others, 1948).

Kennedy, Ainsworth and Toms (1948), in their experiments, suspended the specimen from the radial arms of a "roundabout" driven by a gramophone motor. The "flying" speed was, therefore, imposed upon the insect and, as it was travelling on a circular path, the abdomen was bent outwards, due either to centrifugal force or to an effort by the locust to right itself on to a straight course. The straight abdomen found in natural flight can only be obtained in still air by moving the locust forward in a straight line. This requires a very long track for spraying experiments and even then, an airspeed is imposed upon the specimen from without. The alternative of suspending the locust in a moving air stream whose speed can be varied until it is equal to the natural airspeed of the specimen offers several advantages, including compactness. In addition, under the stimulus of the sensory hairs on the frons and vertex described by Weis-Fogh (1950), the locust will normally orientate itself directly upstream and so be in a convenient attitude for spraying. These conditions can be realised by use of the wind tunnel and flight balance described below.

---

* Now at Ministry of Supply.

The wind tunnel.

A circular-section wind tunnel, with windspeeds continuously variable up to 7 metres per second (16 miles per hour) was constructed as shown diagrammatically in fig. 1. The intake and working sections were formed in Perspex which, being transparent, facilitated the investigation of responses to visual stimuli and reduced the possibility of " fixed points " within the visual range of the locust interfering with its natural behaviour. As the wing span of *Schistocerca* is about six inches and it was desirable to have a relatively uniform windspeed and spray-droplet distribution over this width, the working section of the tunnel was made 12 inches in diameter. The flared intake was designed to aid rapid acceleration of the air and spray droplets so that the latter arrived in the working section at the correct angle of approach to the locust.

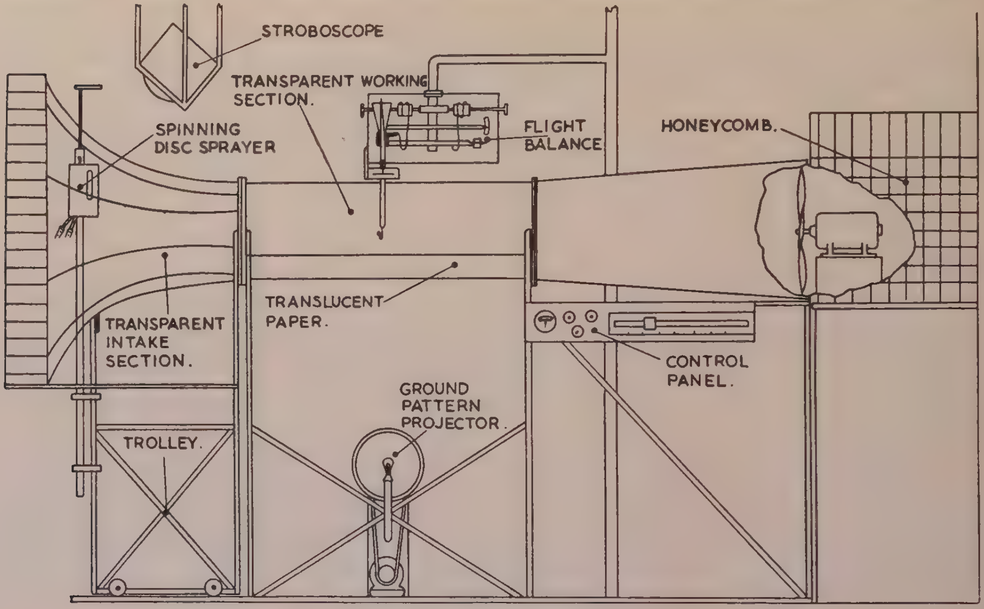


Fig. 1.—Wind tunnel.

The tunnel was housed in a small room to economise on the heating required to maintain the temperature at 28°–32°C. The smallness of the room tended to give rise to considerable turbulence but this was satisfactorily minimised in the tunnel by the use of honeycombs at the front of both sections and around the propeller housing.

The intake section was mounted on a trolley so that it could be pulled forward whilst the locust was placed on the flight balance.

The flight balance.

The balance (Pl. IX) was designed to measure simultaneously the pull or drag of the locust and its "lift". The insect was suspended from the hook at the lower end of the rod A, supported at B in gimbals attached to the bracket C. The pull or drag of the locust in the direction of flight was measured by the deflection of the upper end of A over the scale D. By virtue of the gimbal mounting, the rod A was also free to move at right angles to the line of flight and so impose the minimum restraint upon the locust. Deflection in this direction was indicated by the scale E. The bracket C was carried on pivots attached to the ends of the beams F and G which were in turn pivoted at their centres on the central column H. The beam F acted as an ordinary balance indicating the apparent weight or upthrust of the locust by the pointer moving over the scale J. Beam G kept the bracket C in an upright position. Too violent movement of the balance arms in any direction was resisted by the vane-in-oil dampers K, K^1.

In order to avoid vibration, the balance was suspended from a rigid support free of the wind tunnel with only the lower end of rod A actually inside the tunnel. A "null" method was adopted for using the balance. Any forces exerted on the balance by the locust or by the wind in the tunnel were offset by means of two chains fed from the drums L and M. One chain restored the vertical arm A to zero to counter any drag or pull of the locust and the second chain restored the beam F to zero if the locust weighed down on the hook or thrust upwards. Drum L was calibrated for weight on the hook and drum M for the amount of chain required to offset the drag of rod A at any given windspeed with no locust attached to the hook.

In making an observation of locust airspeed, an insect was attached to the hook and the windspeed gradually varied, with appropriate adjustments to the reading of drum M (offsetting the drag of rod A), until the pointer on scale D returned to zero. At this windspeed the locust was neither dragging nor pulling forward. Similarly, if drum L indicated zero weight on the hook when the pointer on scale J was returned to zero, the locust was virtually behaving as in natural flight and entirely supporting its own weight.

The balance had to be constructed in a very robust fashion to withstand the quite considerable jerking that it received when a locust became excited and its flight in consequence very erratic. Despite this robustness its sensitivity was such that a full scale reading of drum L corresponded only to a weight of 3 grams on the hook at zero windspeed.

Method of suspending the locust.

Experiments were carried out to ascertain the most suitable form of suspension. Kennedy, Ainsworth and Toms (1948) used loops of thread around the pronotum and thorax and a clip gripping the pronotum. Since wing beating is effected by movement of the thoracic wall under muscular contraction, any type of support such as that mentioned above which would restrict or hamper this movement was considered undesirable. In the early experiments the pronotum of the locust was waxed directly to the vertical arm of the balance with provision for adjusting the angle of the locust to the horizontal. Although this gave greater freedom, it was unsatisfactory as the locust was still unable to set its own angle in flight. Various types of hooks and light wire loops attached to the pronotum by the smallest practicable amounts of wax were therefore tried out and the combination eventually adopted can be seen in Pl. X. This consisted of a 28 S.W.G. stainless steel wire loop attached to the pronotum and passed over a spiral hook at the bottom of the vertical arm of the balance. The hook was given this shape to prevent the loop coming off when the locust thrust upwards. The wax used for attachment of the loop consisted of a mixture of three parts beeswax and one part colophonium resin (rosin) with a melting point of 60°C.

Observations showed that as the freedom of suspension increased and the loading on the pronotum decreased the flight performance generally tended to improve. For instance, among the factors that could be directly measured, the wing-beat frequency increased from 18–20 cycles per second with a rigid suspension to 22–24 cycles per second using the wire loop.

Responses to visual stimuli.

Various visual stimuli, singly and in combination, were investigated in order to obtain the best flight conditions. Unfortunately, no set of conditions was found which would stimulate all the locusts into flight on all occasions. Among the stimuli having some effect were the following.

(i) *Illumination.* The level of illumination of the test room was variable at will. Some specimens preferred a bright surrounding whilst others required total darkness before they would fly. Provision was also made for a limited change in the colour of the illumination. The response to colour varied from specimen to specimen.

(ii) *Ground Pattern.* A light pattern was projected on a translucent paper in the bottom of the wind tunnel and moved backward or forward at variable speed. Some locusts responded to the forward motion and others to the reverse. The nature of the pattern (alternate light and dark stripes, opaque or bright patches or combinations of these in various colours) did not have a marked effect on the response.

(iii) *Shadows.* A light moved over the tunnel casting a shadow of the locust on the paper below it sometimes brought a response.

(iv) *Fixation Light.* Bright illumination of the wall at the end of the wind tunnel ahead of the locust or an electric lamp some distance in front of it had no positive effect.

(v) *Flashing light.* Rapid flashing of an electric lamp or of a stroboscope directed at the locust sometimes elicited a flight response.

(vi) *Rapid movement.* Rapid movement of, for example, the hand at the side of the tunnel occasionally gave rise to a response.

In general any one of these stimuli which was effective on the first occasion soon lost its effectiveness when repeatedly applied. Since no optimum combination of stimuli could be evolved, each locust was treated individually until a good flight response was obtained.

Experimental criteria of "natural" flight.

As a result of being handled the locust was always a little unsettled on first being put into the wind tunnel and was, therefore, allowed time to settle down with the wind speed maintained at 3 metres per second. The various stimuli were then applied and the windspeed adjusted until the following conditions, taken as an index of "natural" flight, were satisfied:

(i) the hind legs were bent up to lie alongside a straight abdomen, the middle legs trailed against the hind legs and the front legs were drawn up against the sides of the pronotum (see Pl. X);

(ii) the body maintained a small but constant inclination to the horizontal;

(iii) there was no drag or pull registered on the flight balance; and

(iv) the weight or upthrust on the hook was a minimum.

In the experimental flights, the conditions (i), (ii) and (iii), once set, remained reasonably constant for any given specimen, but (iv) was frequently subject to sudden variation, probably connected with the undulating flight of the locust in the field.

When these criteria were satisfied the suspending loop could be seen to be oscillating, with the frequency of the wing beats, about a mean position on the hook. For the greater part of the cycle the loop was clear of the hook indicating that "natural" flight had been attained. To prevent the locust from swinging upwards and clinging to the suspension arm of the balance the loop had to be kept small in diameter—comparable with the amplitude of the oscillation. In these circumstances a small reaction was sometimes recorded on the flight balance even though the locust was in "natural" flight.

Material.

Supplies of locusts were drawn at intervals from stocks reared at the Anti-Locust Research Centre, supplemented occasionally by supplies from other sources. The age of the insects at this stage was about seven days after the last moult. They were used experimentally between two and four weeks after the last moult. During this time they were kept in cages about 18 inches cube fitted with a 15-watt electric bulb to give radiant heat during the day. The temperature during the day was about 30°C. (relative humidity 45 per cent.) and fell to about 18°C. at night, giving, as near as practicable, the diurnal variation in the field. The locusts were fed each day, one hour before the temperature began to drop, with fresh green grass or cabbage, according to the season. Dry bran was always available in the cage.

Flight performance.

Flight experiments were carried out over the temperature range 25–30°C. with a mean of about 28°C. The duration of flight varied from a few minutes to over five hours, the same specimen performing differently on successive occasions. The extremes of airspeed observed were 2·5 and 6·5 metres per second, but these were exceptional and the great majority lay between 3 and 5 m./sec. (6·5 and 11 miles per hour) with an overall average of 3·2 m./sec.

Measurement of Horizontal Equivalent Area.

Definition.

The Horizontal Equivalent Area (HEA) has been defined as the horizontal plane area which, when passed through a curtain of droplets of a given diameter with the same velocity as a locust, collects the same number of droplets as the locust. It is an analytical device used to calculate spray expenditure in the field and bears no direct relation to the plan area of the locust. The aerial curtain itself contains a wide range of droplet sizes, but these are distributed through a considerable depth of swarm and each locust as it passes through the curtain encounters only droplets of a very small size range. The dose picked up by each locust is the product of the sedimentation rate and the HEA. Before the lethal effectiveness of the curtain as a whole can be calculated, it is necessary to know quantitatively how the HEA varies with droplet size.

Of the many factors which contribute to the HEA value, all but one are directly associated with the locust itself—hence the necessity for "natural" flight conditions in the wind tunnel. The important external factor is the angle of approach of the droplet to the locust, determined by the ratio of the horizontal velocity of the locust to the vertical velocity of the droplet. It varies with locust airspeed and droplet size as shown in fig. 2.

Production of spray in the wind tunnel.

A spray, homogeneous in droplet size, was obtained from a spinning disc sprayer of the type described by Walton and Prewett (1949) in which the size of the droplets is determined by the peripheral speed of the disc. In the present experiments three discs, mounted one above the other, were necessary to give a spray of sufficient extent to fill the volume swept out by the wings of the locust. The discs were driven by an air turbine and their speed measured by a quadrant disc and stroboscope (fig. 3). The spray liquid was fed to the discs at a standard rate from a 20 ml. hypodermic syringe operated by an electric motor.

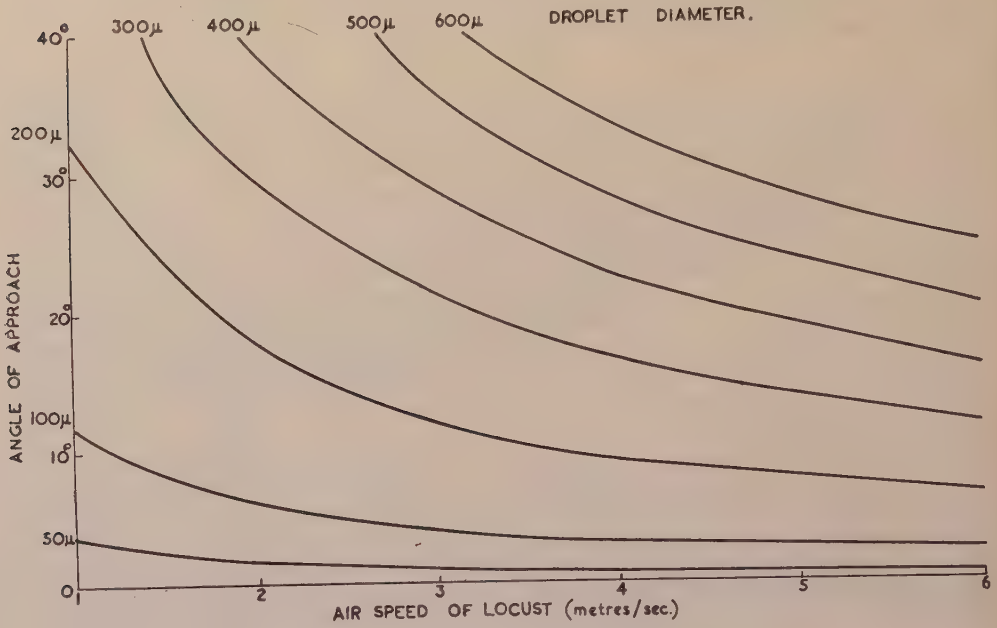


Fig. 2.—Angle of approach of droplets to a locust in flight.

The sprayer was held in place in the intake of the tunnel and raised or lowered according to the droplet size and wind speed so as to give, for the smaller droplets, the correct angle of approach of the droplets to the locust. With the larger droplets complete adjustment could not be obtained, but the maximum error introduced did not amount to more than about 2° when the angle of approach was 20°, corresponding to an overestimation of about 4 per cent. in the value of the HEA.

Experimental procedure.

To simplify the procedure and to avoid handling relatively large quantities of toxic Mk. IV DNC solution, the HEA measurements were carried out with a lubricating oil, containing Grasol Blue as a characteriser, of physical characteristics very similar to those of the Mk. IV solution.

A flat plate (approximately 10 × 7 cm.) was placed horizontally in the wind tunnel in the position normally occupied by the locust. With the sprayer positioned according to the selected wind speed, the standard quantity of oil at a given droplet size was sprayed into the tunnel. The oil collected on the plate was washed off with 10 ml. of xylene and estimated quantitatively with a Unicam colorimeter. From this the pick-up by one square centimetre horizontal plane area was determined. The process was repeated for a range of wind speeds and droplet sizes and the results graphed.

The locust whose HEA was to be measured was suspended from the flight balance and conditions adjusted until "natural" flight was obtained. After the sprayer had been positioned to suit the particular airspeed of the locust, the standard quantity of oil was emitted as droplets of a selected size. The locust was then removed from the wind tunnel and shaken in a bottle containing 10 ml. of xylene. This removed the oil which had been picked up by the locust and enabled the quantity to be estimated with the colorimeter. Previously, by applying known quantities of the oil to locusts, it had been shown that this method of estimation gave results correct to within 5 per cent., the extraction of pigment comparable with Grasol Blue being insufficient to interfere with the results.

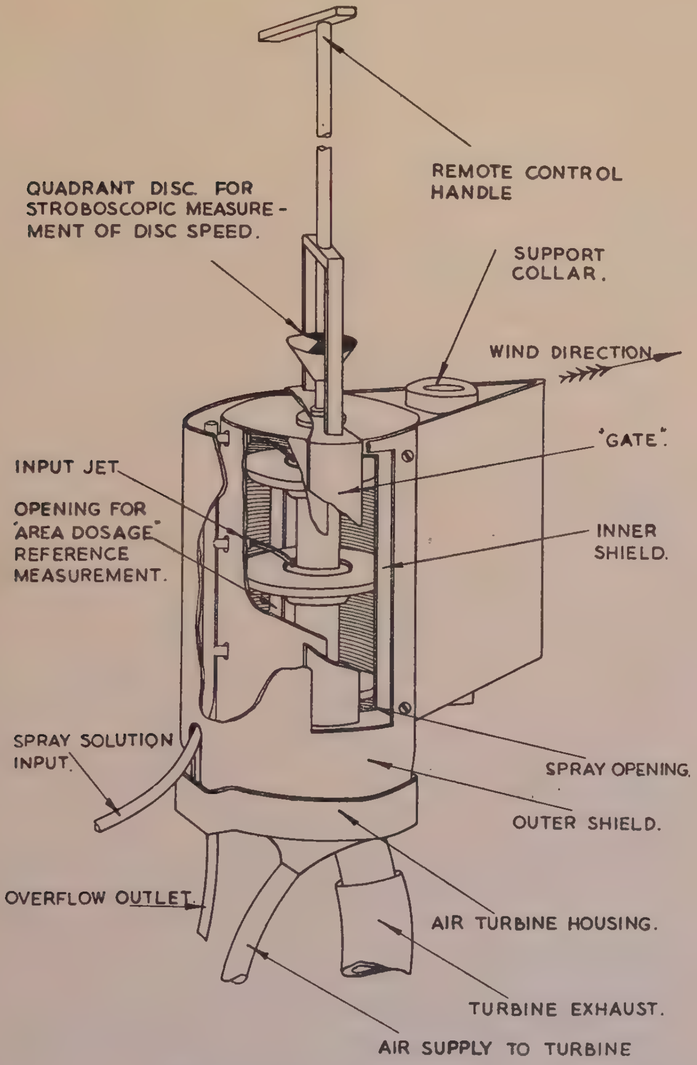

REMOTE CONTROL HANDLE
QUADRANT DISC. FOR STROBOSCOPIC MEASUREMENT OF DISC SPEED.
SUPPORT COLLAR.
WIND DIRECTION
"GATE".
INPUT JET
OPENING FOR "AREA DOSAGE" REFERENCE MEASUREMENT.
INNER SHIELD.
SPRAY SOLUTION INPUT
SPRAY OPENING.
OUTER SHIELD.
OVERFLOW OUTLET
AIR TURBINE HOUSING.
TURBINE EXHAUST.
AIR SUPPLY TO TURBINE

Fig. 3.—Triple spinning disc sprayer.

From the measurements of pick-up by the locust and by one square centimetre of the horizontal plate under similar conditions, the HEA was calculated. A

TABLE I.

Droplet diameter (μ)	Mean HEA (cm.^{2})	Standard deviation	Mean airspeed (m./sec.)	No. of expts.
50	445	155	3·8	14
100	110	33	3·5	13
200	46	10·3	3·2	14
300	31	4·5	3·3	21

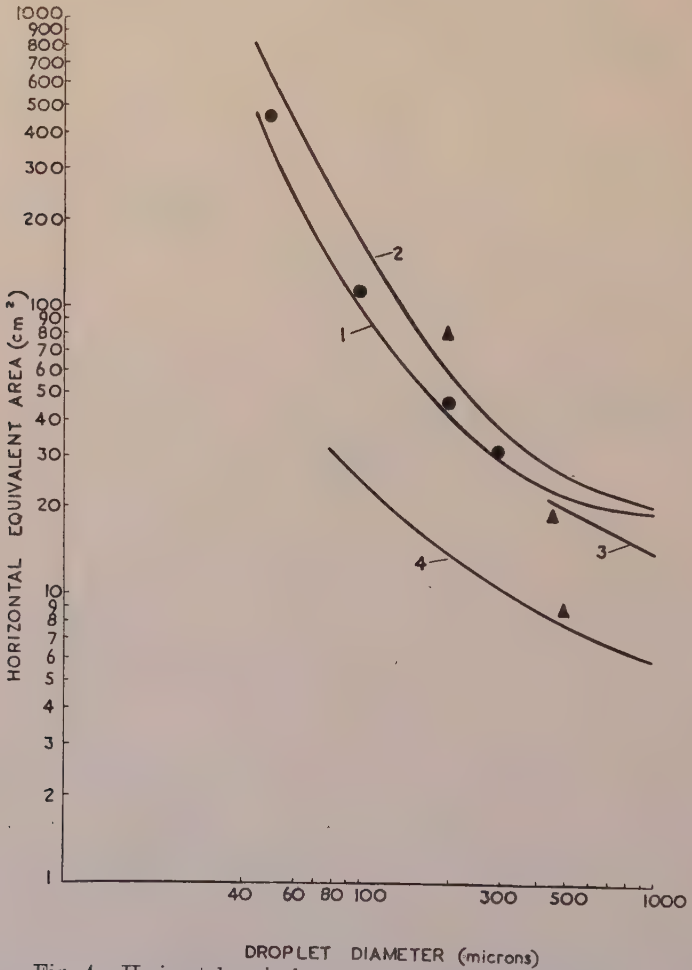


Fig. 4.—Horizontal equivalent area as a function of droplet size. Values calculated from equation (1) (see page 187).

(1) 3 metres/sec.
(2) 5 metres/sec.
(3) Calculated average values allowing for re-dispersion (see page 186).
● Average experimental values.
▲ Values from Kennedy & others (1948).
(4) Values from Sawyer (1950).

summary of the results is given in Table I and fig. 4. Measurements were completed with droplets of 50, 100, 200 and 300 microns diameter *, but droplets of greater diameter could not be used without altering the position of the flight balance. It was decided, therefore, to proceed with toxicity measurements covering the same size range and to resume with HEA measurements for the larger droplets at a later date. Ultimately it was found that these measurements were complicated by the re-dispersion of large drops by the wings in flight as discussed below and, when this had been qualitatively investigated, insufficient time remained for further HEA measurements. As will be shown later this does not detract seriously from the value of the work.

Re-dispersion of large drops by the wings during flight.

Examination of the stain shapes on the wings of locusts resulting from hits by large drops showed that some of the liquid of the original drop was thrown off by centrifugal action. In view of the significance of this effect a short investigation was made to see if there was any quantitative relation between the original drop size, the quantity retained and the size of the re-dispersed droplets.

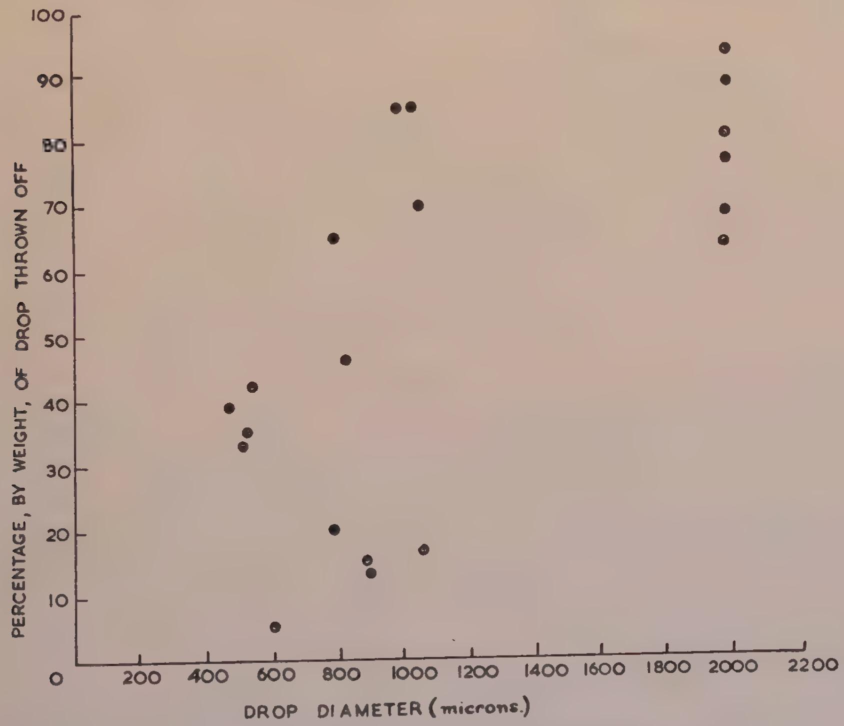


Fig. 5.—Percentage of liquid re-dispersed for a single drop landing on the wing.

These experiments could not be carried out in the wind tunnel owing to the lengthy modifications that would have been required. The locust was, therefore, suspended in still air and stimulated to " flight " by directing a stream of air over the head. Drops of a known size from a microburette were allowed to fall on the wings of the locust from heights of 10 cm. and one metre, and the re-dispersed droplets collected on filter paper rolled into a 12-inch cylinder around the locust. The sizes of the re-dispersed droplets were estimated from their stains on the filter paper.

---

* Droplet sizes are given in diameters throughout.

The results are given in figs. 5 and 6. It was impossible to hit any selected part of the wing at any given time in its cycle. The results in consequence show considerable scatter, but it is evident from fig. 5 that re-dispersion begins in the region of 400μ drops and is quite considerable for drops of 1,000μ (1 mm.). The droplets re-dispersed from the wings cover an appreciable size range (fig. 6).

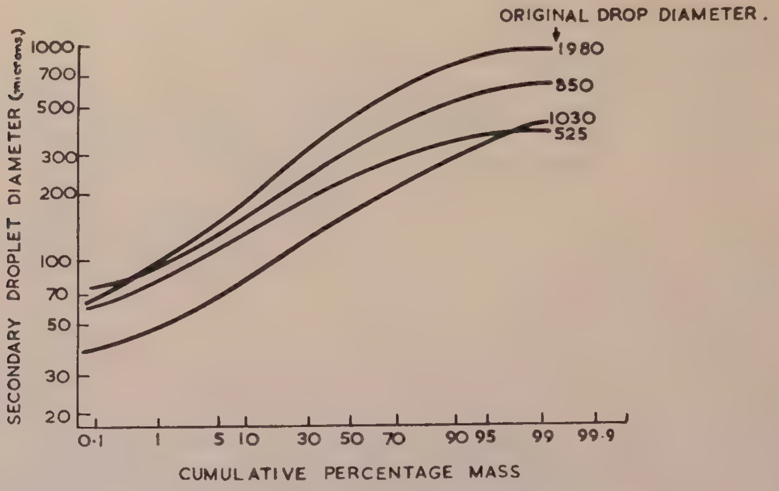


Fig. 6.—Spectrum of secondary drops after re-dispersion of original drops by the wings.

Since it can be shown by geometrical estimation that the wings account for about 80 per cent. of the HEA, the loss of insecticide by re-dispersion may considerably reduce the retained dose for all drop sizes greater than about 300μ. Even at 500 μ, fig. 5 indicates a loss possibly as great as 30 per cent. In this region, therefore, the HEA as a means of determining the quantity of spray intercepted and the quantity retained, ceases to have the single value it has for smaller droplet sizes. With the larger drops, the HEA for the intercepted dose can be expected, from the analysis given below, to tend steadily towards a limiting value whereas the retained dose will, in individual cases, vary over a wide range as suggested by fig. 5. It follows that the value of the HEA for the larger drops could not be accurately determined by the method used for the smaller droplets and that a more precise measurement of the retained dose would require many more experiments than the time available permitted. It was decided, therefore, to use calculated values of the HEA for droplets greater than 300μ and to make approximate corrections for the retained dose from fig. 5.

Geometrical estimation of HEA.

The HEA is by definition the horizontal area which collects by sedimentation alone the same number of droplets as the locust collects by sedimentation and impaction. The calculation of the dose by sedimentation in any given case is relatively simple, but any rigorous treatment of impaction is difficult, as Townsend (in Kennedy, Ainsworth & Toms, 1948) has shown, owing to the lack of suitable data. An approximate allowance for impaction can, however, be made by adding to the plan area of the locust the projected horizontal area of the surfaces on which impaction takes place and then treating the problem as one of sedimentation only. If the angle of projection is taken as the angle of approach of the droplets to the locust (fig. 7) the following expression is obtained:—

$$HEA = BP + 0{\cdot}5\,E^2 + CL \cot \alpha + \phi(\mathrm{d})\,E \cot \alpha \ldots \qquad \ldots \qquad (1)$$

where B = overall length; P = body width;
E = elytron length;
C = width of head; L = length of head;
α = angle of approach of droplet to locust;
and ϕ(d) is to be obtained from the experimental measurements (see below).

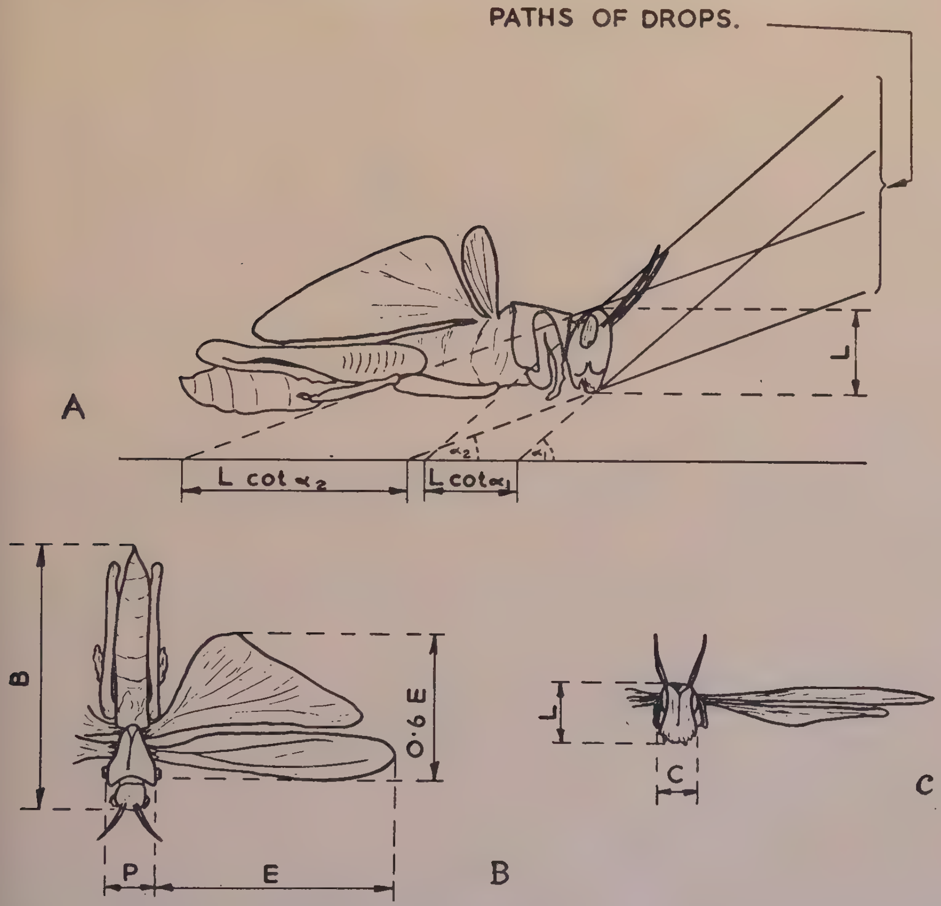


Fig. 7.—Geometrical estimation of horizontal equivalent area from the biometrics of the locust.
A. Showing variation of the horizontal equivalent of a vertical measurement projected at various angles of approach of droplets.
B. Horizontally projected area.
C. Vertical areas presented to droplets.

The coefficient of the second term is obtained by regarding the two wings on one side of the body as forming a triangle of base E and height 0·6E, giving an area of 0·3E². Hence the total wing area is 0·6E². When the wings are beating, however, the area projected on a horizontal plane is less than this. From the wing motion as described by Kennedy, Ainsworth and Toms (1948) it can be shown by graphical methods that the mean projected horizontal area in each cycle is 0·83 of the true area. Hence, $0{\cdot}6E^2$ above becomes $0{\cdot}5E^2$ in equation (1).

Numerical values of the coefficient ϕ (d) in the last term have been obtained from the difference between the first three terms of equation (1) and the experimentally measured HEA for each droplet size. These are given in Table II below together with the best estimates of values for larger droplets obtained by extrapolation.

TABLE II.

Droplet diameter (μ)	ϕ (d)
50	1·19
100	1·10
200	1·00
300	0·80
500	0·60*
1000	0·40*

* Extrapolated values.

Solutions of equation (1) with locust airspeeds of three and five metres per second are given in fig. 4 for a random sample of locusts whose average biometrics were: E = 5 cm.; BP = 4·3 cm² and CL = 0·8 cm². The value of α was obtained from fig. 2.

Discussion of results.

The pace of the work was largely determined by the behaviour of the locusts and there were frequently periods of several days when suitably sustained flight could not be obtained. Conditions in this respect were worse than in the earlier work when the experimental requirements for " natural " flight were being investigated. The number of experiments performed at each droplet size was therefore small in relation to the number of variables involved and insufficient to enable the sexes to be dealt with separately. It was intended to remedy this at a later stage but the time available did not permit. Since the locust determined the airspeed for a given experiment, it was not possible to cover methodically a set of observations at selected airspeeds. With these limitations and the variability of the material, the results show a wide range of variation (actual data deposited in the files of the Ministry of Supply and of the Anti-Locust Research Centre) and the mean value of the HEA for a given droplet size is the only figure adequately determined.

The results give a good indication of the effect of droplet size on the HEA but give no direct estimate of the effect of airspeed except to show that it is largely masked by the effects of other variables. Some indication of its magnitude can be gained from curves 1 and 2 in fig. 4, calculated from equation (1). The change of airspeed from three to five metres per second adds about 10 per cent. to the HEA for the larger droplets and about 80 per cent. for the smaller ones.

Since the experimental points lie in a proper relation to curves 1 and 2, extrapolation of these curves forms the best method of estimating the HEA for 500μ and larger drops. It should be noted that from the form of equation (1) the HEA tends asymptotically to 17 cm² for very large drops. These extrapolated values, however, apply strictly only for the intercepted dose. The HEA for retained dose, after allowing approximately for re-dispersion (fig. 5), lies somewhat lower, in the position suggested by curve 3 of fig. 4.

For comparison purposes, the HEA values quoted by Kennedy, Ainsworth and Toms (1948) and by Sawyer (1950) are included in fig. 4. At 200μ and 450μ, there is good agreement between present values and those given in the first of those papers, although the species used was different. The sharp decrease in HEA for droplets of 500μ shown by Kennedy, Ainsworth and Toms is not supported by present values and seems to be too rapid a differentiation for so small a change in droplet size. It would be difficult to attribute this entirely to the effect of re-dispersion.

After allowing for the fact that the values quoted by Sawyer (1950) were determined for the smaller species (*Locusta*), there still remains a serious difference between curve 4 of fig. 4 and the other results. The steep slope of curves 1 and 2 indicates that collection by impaction on the vertical surface of the locust becomes increasingly important as the droplet size, and therefore the angle of approach to the droplet, decreases. In this increased pick-up the wings play an important part and changes in amplitude or frequency of wing beats could appreciably affect the result. The difference between curve 4 and the results of the present experiments is probably due largely to this factor. With experience of the characteristics of natural flight gained from the present experiments, it is clear, in retrospect, that locusts tethered to a roundabout in the earlier experiments were in a most unnatural condition. On the whole therefore the present values are regarded as better estimates of the HEA than those previously put forward.

Measurement of Toxicity as a Function of Spray Droplet Size.

Objective.

In the theoretical treatment given by Sawyer (1950), it was assumed that equal amounts of insecticide picked up by locusts were equally toxic independently of the droplet size and where, as a consequence of this, the poison was deposited on the locust. It was known from the work of Kennedy, Ainsworth and Toms (1948) that this was not necessarily true, but with no other data available an alternative assumption could not be made. The object of the present experiments was to determine directly how the quantity of poison for a given lethal effect varied with the droplet size in which it was applied.

Material.

The insecticide used in these experiments was DNC in the form of Mk. IV solution. This consisted of 20 per cent. (by weight) of DNC, 72 per cent. Iranoline 2241 and 8 per cent. Kerosene Extract Bottoms. To facilitate colorimetric measurements, 0·5 per cent. by weight of Waxoline Red was added to the solution.

Apparatus and experimental method.

For simplicity in the HEA measurements, a relatively large dose could be applied, but in the toxicity measurements it was necessary to apply a very small and variable fraction of this dose with the same accuracy, *i.e.* of the order 10^{-6} gm. per second from each disc. An output as low as this could not be achieved with adequate control and the practical minimum was about 30×10^{-6} gm. per second, giving, for the lower doses, a spraying time of only a few seconds. To keep the variations to a minimum, the sprayer was maintained in continuous operation and the entry of spray into the wind tunnel was controlled by a gate inside the outer shield of the sprayer (fig. 3) which could be rapidly opened and closed by hand. The opening of the gate simultaneously uncovered a strip of filter paper behind a second slit in the outer shield. The output of spray into the wind tunnel was calibrated against the amount picked up on this strip of filter paper.

Owing to the very short spraying time involved and the added complication that the airspeed of the locust could not be known until the experiment was in progress, no two locusts received the same dose. Finally, the doses actually picked up covered the whole range by a series of small increments instead of being grouped closely around predetermined values at wider intervals in that range.

Apart from the modifications to the sprayer, the method of experiment was essentially similar to that described on pp. 182–183 for measurement of the HEA. After spraying, the locusts were put separately into recovery cages and the mortality after 24 hours observed. The biometrics of the dead and surviving locusts were taken and the HEA calculated from equation (1) on p. 187. From this and the corresponding output from the sprayer the total quantity of spray material picked up by each locust was calculated.

Results.

For the reasons given on pp. 193–194, the results are presented here in terms of the mass sedimentation rate, S, used in equation (3) below. It is obtained for each experiment by multiplying the directly measured mass sedimentation rate on a square-centimetre horizontal plane in the wind tunnel by the airspeed of the locust. It corresponds to the rate of sedimentation on one square metre in the metre-thick ideal curtain (Sawyer, 1950).

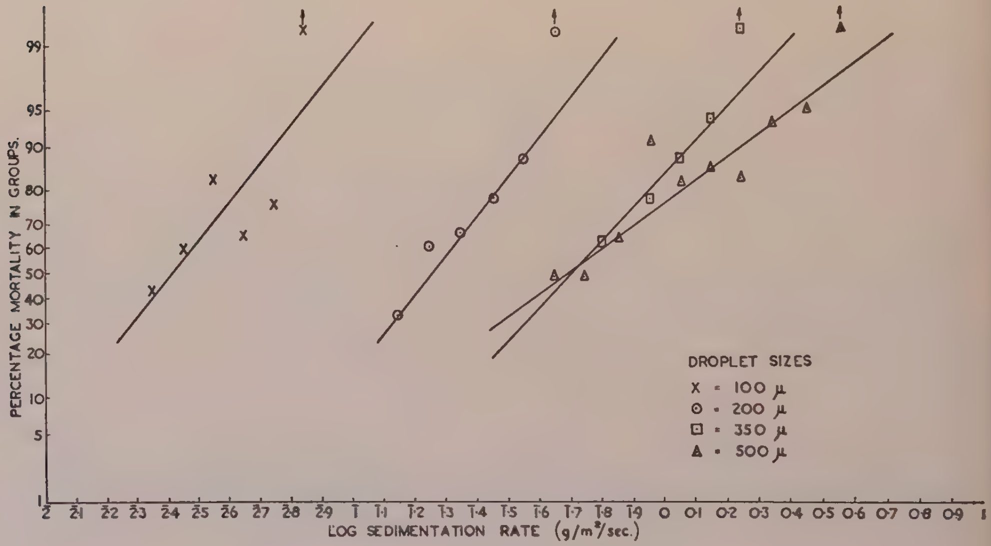


Fig. 8.—Calculation of LD99, LD90, etc.

The experimental results were arranged in ascending order of log. sedimentation rate for each droplet size and divided into a convenient number of groups. The percentage mortality in each group was plotted against the mean log. dosage of the group (fig. 8). From these curves the value of S required to give mortalities of 99, 90 and 50 per cent. (LD99, LD90 and LD50) were read off and plotted as a function of droplet size (fig. 9).

Although fig. 9 gives the data in the most suitable form for field use, it is not in units which can be easily compared with previous work. Such a comparison can be made from fig. 10, derived from fig. 9 by multiplying throughout by $\frac{(HEA)}{u\ w}$ (where u is the locust airspeed in m./sec. and w is the average weight of the locust in grams). This gives the toxic efficiency of the spray in terms of the quantity required per gram weight of the locust. It should be noted that the variation in toxicity with locust airspeed is relatively small.

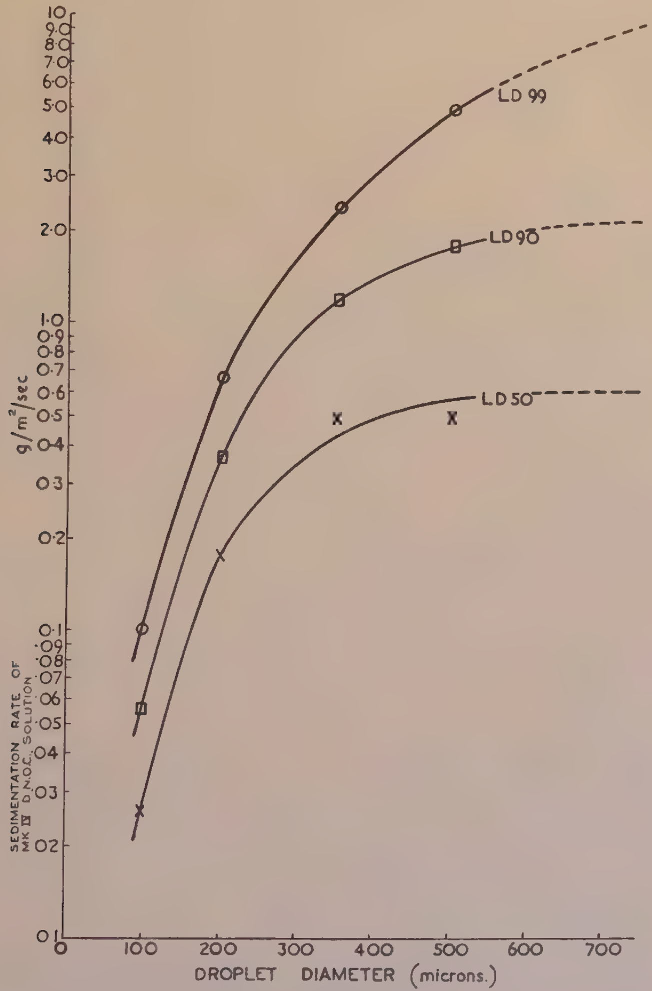


Fig. 9.—Toxic efficiency of Mk. IV DNC solution in terms of sedimentation rate.

Discussion of observations.

Throughout the toxicity measurements there was no characteristic response by the locust to being sprayed. In the great majority of cases the locusts continued flying " naturally ". In a few instances, one or both of the hind legs were extended and very occasionally flight ceased altogether (when the experiment was abandoned). Since similar effects were also observed during the HEA measurements, they most probably arose as a response to being sprayed rather than to the toxicity of the spray. As, by the method of experiment adopted, the locust was removed from the wind tunnel within a few minutes of being sprayed, there was no opportunity of studying any long term effect of the spray upon flight. When placed in the recovery cage, the locust behaved in a way more characteristically related to the dosage it had received. Very broadly, if the dose had been a light one, its behaviour differed little from that of an undosed locust and there was no noticeable change in activity. With doses around the middle of the range used, the locust occasionally wiped its head and antennae with the forelegs but otherwise remained quiescent for several hours until death or recovery. Large doses resulted in repeated wiping of the head and antennae, coupled with a very characteristic walking backwards. This lasted, in some instances, for several minutes, and was followed by a state of quiescence and death within two or three hours. Similar observations on behaviour are reported by Kennedy, Ainsworth and Toms (1948).

It is clear from fig. 9 that the size of the droplets by which the poison is applied plays a vitally important part in the subsequent mortality. A five-fold increase in droplet size, from 100 to 500μ, leads to approximately a forty-fold

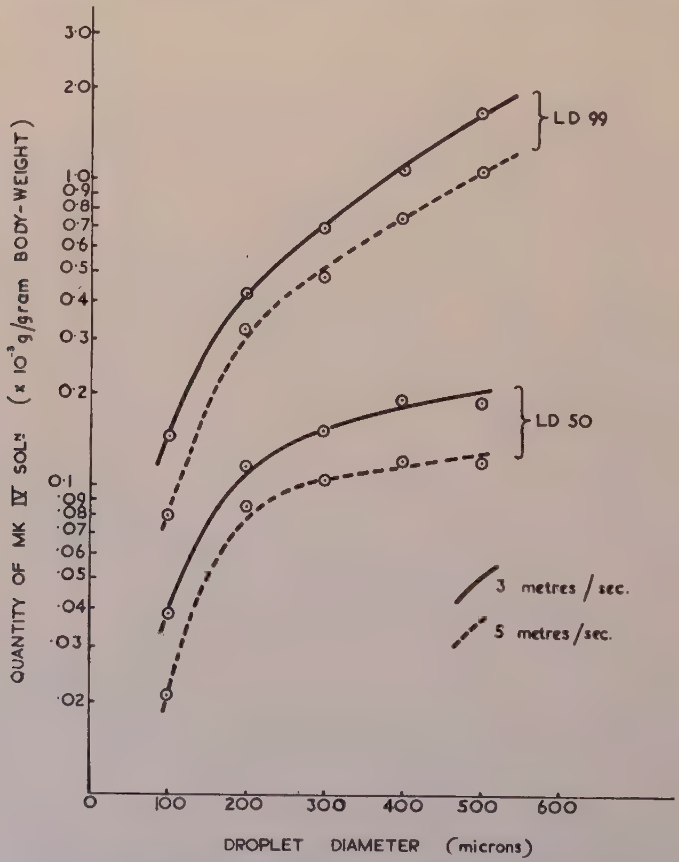


Fig. 10.—Toxic efficiency of Mk. IV DNC solution in terms of the quantity intercepted per gram body-weight of locust.

increase in sedimentation rate for a given effect. The variation is greatest from 100 to 200μ indicating the importance of impaction and also, possibly, an attraction effect as suggested by Townsend (Appendix to Kennedy, Ainsworth & Toms, 1948). For droplets larger than 500μ it is evident from the shape of the curves that the effect of droplet size is much reduced and up to at least 750μ the appropriate sedimentation rate can be obtained by extrapolation with sufficient accuracy for the calculation of such diagrams as fig. 11.

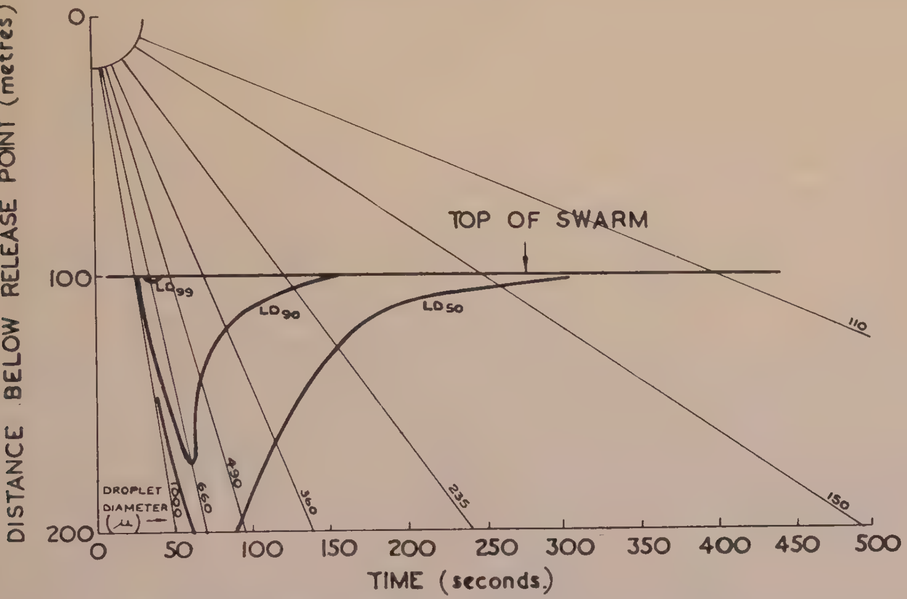


Fig. 11.—Lethal zones within a swarm of 5 locusts per metre^3 using a coarse spray (mass median diameter 400μ) output 300 gm./metre run.

A similar but somewhat reduced trend is shown in fig. 10 as droplet size increases. Allowance for the change of the HEA and hence of the total pick-up having been made in this diagram, the variation in toxic effect with droplet size must be very largely due to the more vulnerable areas on which the droplets are impacted and their more even distribution. The very pronounced increase in the toxicity of 100μ droplets is particularly noteworthy. From equation (1) the change in the amount impacted on the head does not appear sufficient to account for the whole of the increase, so that a significant contribution must be made by the more even distribution. Fig. 10 leads generally to the conclusion that the head is relatively more susceptible than previous work (Kennedy, Ainsworth & Toms, 1948) would suggest. The general level of toxicity compares reasonably with the only other information available. Kennedy, Ainsworth and Toms (*loc. cit.*), working with *Locusta* and a 2·5 per cent. solution of DNC, estimated the median lethal dosage for 500μ droplets to be 15 micrograms of DNC per gram body-weight of mixed sexes. The present experiments give a corresponding mean value of 30 micrograms of DNC for *Schistocerca*. This difference may be due to the species involved or it may indicate that the toxicity of the solution is not directly proportional to its DNC content.

Application to Aerial Spraying of Flying Swarms.

Since the lethal effect of a given quantity of insecticide can no longer be regarded as independent of the droplet size and since the present values of HEA for *Schistocerca* are much larger than those previously used, it is of interest to consider in some detail how far certain of the conclusions of Sawyer (1950) relating to field applications are affected by the results of the present work.

The quantity, Q, of spray picked up by a locust flying in a swarm was given as:—

$$Q = \frac{V^2}{Du} \cdot \frac{\delta W}{\delta V} \cdot A_{(d,u)} \left\{ - \exp. \left[n(D - D_o).A_{(d,u)} \right] \right\} \text{ (grams)} \quad \ldots \qquad (2)$$

where V = mean terminal velocity (m./sec.) of droplets of an elementary range of mean diameter, d,
δV = difference of terminal velocities of droplets at the ends of that range,
δW = weight of spray (gm.) put out as droplets within that range,
u = locust airspeed (m./sec.),
$A_{(d,u)}$ = HEA of the locust for the particular droplet size and airspeed,
D = distance (m.) below the release point of the spray,
D_o = distance of the top of the swarm (m.) below the release point,
and n = number of locusts per cubic metre of swarm.

Using this equation, the depth to which a given dosage level penetrated a swarm was calculated for typical cases and the results presented in diagrammatic form.

In the present experiments the sedimentation rate, S, for a given lethal effect was directly measured, whilst Q could only be obtained indirectly. It is preferable therefore to use the substitutions given in the original paper and to re-write equation (2) as

$$S = \frac{V^2}{D} \cdot \frac{\delta W}{\delta V} \left\{ - \exp. \left[n(D - D_o).A_{(d,u)} \right] \right\} \quad \ldots\ldots\ldots\ldots\ldots\ldots \qquad (3)$$

into which the experimentally measured quantities can be directly inserted.

It is not necessary here to give complete solutions of equation (3) for all the cases discussed in Sawyer's paper. The general trend of the modifications introduced by the new experimental values can be obtained by considering the two typical cases, illustrated in figs. 11 and 12. These have been calculated for the "coarse" and "fine" sprays (mass median diameters of 400μ and 200μ, respectively), using the values of n = 5 locusts per cubic metre and D_o = 100 metres, corresponding to figs. 3 and 4 of Sawyer (1950). With the information now available from the experimental work, figs. 11 and 12 have been contoured directly in terms of LD50, LD90 and LD99.

For the coarse spray, the contours of fig. 11 closely resemble in general shape those of fig. 3 of Sawyer (1950) but as the LD50 for 500μ droplets now corresponds approximately to 400 × 10^{-6} gm. of solution instead of 125 × 10^{-6} gm., the lethal dosage does not extend so deeply into the swarm in fig. 11 as the original analysis suggested. The latter value was based on toxicity by injection so that some disparity was bound to occur. In addition it has been shown (see p. 186) that up to 80 per cent. of the dosage may be picked up by the wings and if this fraction is assumed to be largely ineffective in killing the locust the disparity between the two sets of data disappears.

In fig. 12, on the other hand, the lethal zones vary in shape considerably from those given in the earlier calculations due to the rapid increase of lethal effect with decrease in droplet size below 200μ. The full effect of this increased toxicity is, however, offset by the corresponding rise in the HEA, which increases the attenuation factor, so that a given swarm tends to become more "opaque" as the droplet size decreases. The two factors combine to give lethal zones which do not extend very deeply into the swarm, but which maintain a fairly constant lethal effect over a relatively long time.

Comparing figs. 11 and 12 it will be seen that the differences in performance between the coarse and fine sprays anticipated in the earlier work have become accentuated when the present experimental values are inserted. The contours of the coarse spray have become narrower and more sharply peaked with a consequent shortening of the renewal interval to maintain an effective curtain of spray. The contours are in fact not suitably shaped for efficient overlapping and it is questionable whether the technique of aerial curtain spraying as originally conceived could be successfully applied with sprays of this droplet-size distribution except over a narrow range of swarm characteristics.

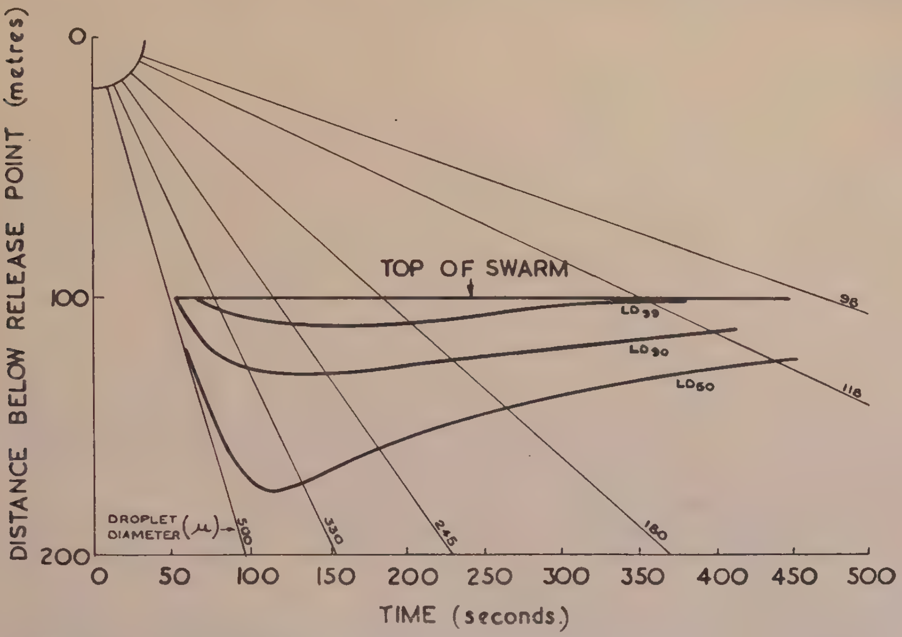


Fig. 12—Lethal zones within a swarm of 5 locusts per metre^3 using a fine spray (mass median diameter 200μ) output 300 gm./metre run.

The current results, however, present the fine spray in a more favourable light than hitherto. It is clearly well adapted for the attack of shallow swarms and permits renewal intervals of such a length that spraying with a single aircraft is quite practicable. Its lack of penetration into the swarm can be partly offset by increasing the output per unit length of spray run but, as the optimum output is about 400 grams per metre, this loses its effectiveness when the depth of swarm exceeds 100 metres.

The change in field technique suggested by the figures is, in effect, that it will be more profitable to attack a swarm layer by layer from the top than by vertical sections from the front. This change in relative suitability of the sprays affects in turn the emphasis to be placed on some of the other conclusions drawn by Sawyer (1950), such as those relating to optimum spraying height and percentage of insecticide usefully applied. A detailed statement of these changes is outside the scope of the present report but they will become apparent when the full set of diagrams, corresponding to fig. 12, are worked out for the particular droplet-size distribution being used in the field.

Summary.

Measurements of the Horizontal Equivalent Area (HEA) of flying locusts and the toxic efficiency of Mk. IV DNC solution, as a function of spray droplet size, have been made using *Schistocerca gregaria* (Forsk.) flying "naturally" in a wind tunnel. The experimental conditions, including visual stimuli, for "natural" flight were determined by means of a flight balance. The observed values of locust airspeed varied from 2·5 to 6·5 metres per second with a mean value of about 3·2 metres per second.

The HEA of locusts in flight was determined by emitting a dyed, non-toxic spray of known droplet size into the wind tunnel in such a way that the angle of approach of the droplets to the locust was the same as that in aerial curtain spraying. The HEA was determined as the ratio of the amount of spray picked up by a locust to the amount collected by unit area of a horizontal test plate under similar conditions. Results showed that the HEA varied with droplet size, decreasing rapidly from 445 cm.^{2} at 50μ-diameter droplets to 31 cm.^{2} at 300μ. HEA values for droplets larger than 300μ were not directly measured owing to the complicating effect of part of the droplets picked up on the wings being thrown off again. It is shown, however, that estimates of the HEA for 500μ–1000μ droplets, sufficiently accurate for all practical purposes, can be made from the measurements at the smaller droplet sizes. The range of locust airspeeds encountered in the HEA measurements was insufficient to determine fully the effect of this factor on the HEA value. An analytical expression has been developed from the experimental values which enables the magnitude of the airspeed factor to be estimated.

The toxic efficiency of the spray as a function of droplet size was determined in a similar way using Mk. IV DNC solution in place of the dyed oil. The LD50 increased from 6 micrograms DNC per gram weight of locust at 100μ to 30 micrograms at 500μ, most of the change taking place between 100 and 200μ. The change of airspeed from 3 to 5 metres per second increases the toxicity by a factor varying with droplet size between 40 and 90 per cent. The increased effectiveness of the smaller droplets appears to be due to collection on the head and a more even contamination.

When the experimentally determined values are used to calculate the expenditure of spray required in field operations, it is evident that a coarse spray (mass median diameter 400μ) is on the whole less effective than a fine spray (mmd 200μ), and it appears that greater efficiency will be obtained by attacking a flying swarm layer by layer from the top rather than by vertical sections from the front as originally envisaged in aerial curtain spraying.

Acknowledgements.

The authors wish to thank Dr. D. L. Gunn for his stimulating advice and criticism and to acknowledge the help received at various times from members of the staff of the Anti-Locust Research Centre. Acknowledgement is also made to the Ministry of Supply for affording the laboratory facilities which enabled the work to be carried out, and to the Chief Scientist, Ministry of Supply, and the Controller, Her Majesty's Stationery Office, for permission to publish this paper.

References.

37 2:3 GUNN, D. L., GRAHAM, J. F. & others. (1948). Aircraft spraying against the Desert Locust (*Schistocerca gregaria* Forskål) in Kenya, 1945.—Anti-Locust Bull., no. 4, 121 pp.

37 133. GUNN, D. L., LEA, H. A. F. & others. (1948). Locust control by Aircraft in Tanganyika.—153 pp., London, Anti-Locust Res. Cent.

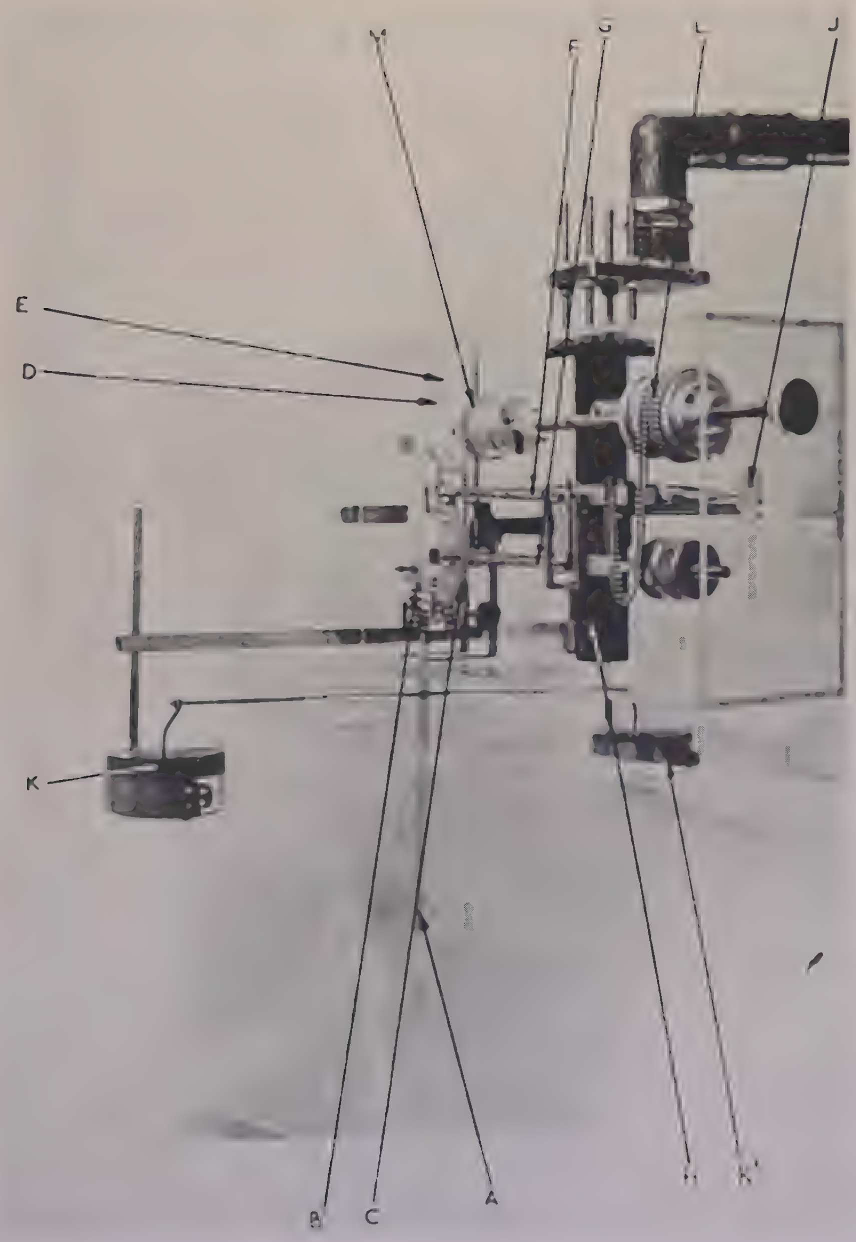
GUNN, D. L., PERRY, F. C. & others. (1948). Behaviour of the Desert Locust (*Schistocerca gregaria* Forskål) in Kenya in relation to aircraft spraying. —Anti-Locust Bull., no. 3, 70 pp.

KENNEDY, J. S., AINSWORTH, M. & TOMS, B. A. (1948). Laboratory studies on the spraying of locusts at rest and in flight.—Anti-Locust Bull., no. 2, 64 pp.

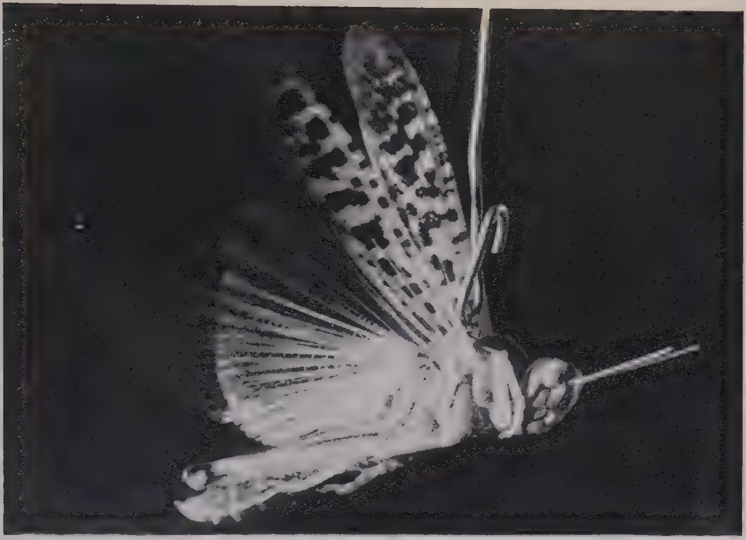
SAWYER, K. F. (1950). Aerial curtain spraying for locust control: a theoretical treatment of some of the factors involved.—Bull. ent. Res., **41**, pp. 439–457.

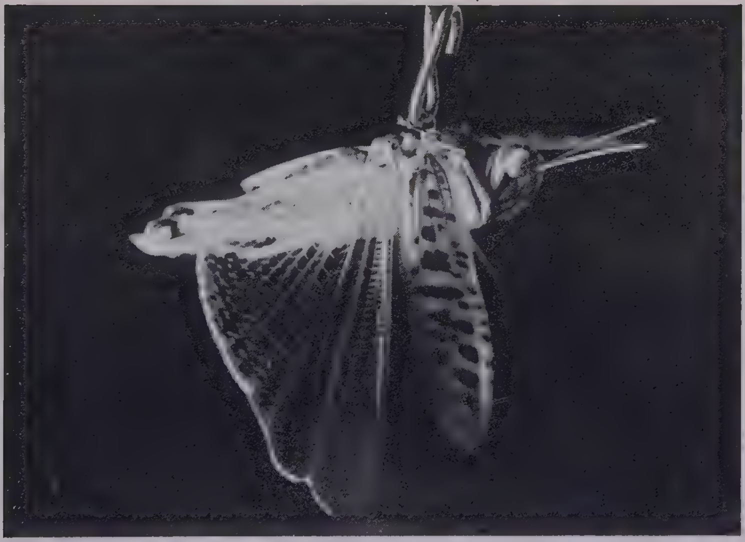
WALTON, W. H. & PREWETT, W. C. (1949). The production of sprays and mists of uniform drop size by means of spinning disc type sprayers.—Proc. phys. Soc. Lond., (B) **62**, pp. 341–350.

WEIS-FOGH, T. (1950). An aerodynamic sense organ in locusts.—Proc. 8th int. Congr. Ent. Stockholm, 1948, pp. 584–588.


M
F
G
L
J
E
D
K
B
C
A
H
K'

THE FLIGHT BALANCE.
(For explanation of lettering see text).





LOCUST IN GOOD FLIGHT POSITION.

Suspended on the flight balance in the wind tunnel.

STUDIES OF THE BITING-HABITS OF AFRICAN MOSQUITOS. AN APPRAISAL OF METHODS EMPLOYED, WITH SPECIAL REFERENCE TO THE TWENTY-FOUR-HOUR CATCH.

By A. J. Haddow.
The Virus Research Institute, Entebbe, Uganda.

Early in 1940 the writer began field work on mosquitos in East Africa. Choice of a particular subject for study being wide, it appeared that perhaps the most important field concerned the biting-behaviour of the female, as this phase of activity (though very important in relation to the transmission of pathogenic organisms) had previously received little attention. In particular, it seemed desirable to investigate the possibility that different mosquito species were active at different times, as it was known that they showed markedly specific behaviour in many other respects.

Work on the biting-behaviour of the female was therefore begun, and the author continued to devote most of his time to this subject until late in 1948. Certain sections of the results have already been published, but by far the greater part has not, and analysis of the final figures is still far from complete. Detailed study of the sample has been carried out in the case of certain species known to be important in relation to disease, or interesting from some other viewpoint, and it seems necessary, before reporting the results, to discuss the progress of the investigation in general terms. This paper is concerned with the methods so far employed, with particular reference to the 24-hour catch, and to such fallacies and difficulties as seem important. To avoid future repetition, a general narrative covering the development of the study is included. It is further necessary to review briefly the results obtained by other workers, and to discuss possible future trends.

List of Species.

To save quoting full scientific names in the text, the following list of the species mentioned, including one Tabanid, is given:—

Anopheles (*Anopheles*) *coustani* var. *ziemanni* Grünb.
,, ,, *implexus* (Theo.)
,, (*Myzomyia*) *gambiae* Giles
Hodgesia cyptopus (Theo.)
Aëdomyia africana Neveu-Lemaire
Taeniorhynchus (*Coquillettidia*) *pseudoconopas* (Theo.)
,, ,, *fuscopennatus* Theo.
,, ,, *aurites* Theo.
,, (*Mansonioides*) *africanus* (Theo.)
Aëdes (*Mucidus*) *nigerrimus* (Theo.)
,, (*Finlaya*) *longipalpis* (Grünb.)
,, ,, *ingrami* Edw.
,, (*Stegomyia*) *aegypti* (L.)
,, ,, *simpsoni* (Theo.)
,, ,, *apicoargenteus* (Theo.)
,, ,, *dendrophilus* Edw.
,, ,, *africanus* (Theo.)
,, ,, *ruwenzori* H. & van S.

Aëdes (Aëdimorphus) irritans (Theo.)
,, *(Skusea) pembaensis* Theo.
Eretmapodites chrysogaster Graham
Chrysops (Kleineana) centurionis Aust.

General Narrative.

In 1940 work was begun at Kisumu, Kenya, and this continued until the end of 1941. The study was concerned almost exclusively with the mosquitos (and particularly with the Anophelines) which frequent native huts. At that time information on biting-activity was exceedingly scanty. Kerr (1933) had made important pioneer studies in West Africa, in which he showed by means of night catches that different species attained their main biting-activity at different times, and Kumm and Novis (1938) had found similar differences in the case of certain diurnal Culicines in South America. Apart from these observations, however, information consisted almost exclusively of scattered comments, based mainly on casual observations made during the course of work on other aspects of mosquito biology. Thus in the case of an exceedingly important African species, *Anopheles gambiae*, though a great deal of information was available concerning many aspects of its behaviour, very little was known about the time of entry to dwellings and the actual biting habits. Evans (1938) in the course of a 29-page summary of the available information on *A. gambiae*, devoted only ten lines of text to the biting-habits and times of biting.

Studies made at Kisumu, mainly in experimental huts, included a long series of catches in which mosquitos were collected hourly throughout the night. These observations (Haddow, 1942) showed clearly that the various species encountered entered dwellings at different times of the night and further, that while some species tended to remain there during the following day, others tended to leave before sunrise.

Numerous difficulties, however, attended the interpretation of the results. Thus, the method employed in the night catches was to make hourly collections of the mosquitos found in the huts. The first and most serious difficulty was that a blood-fed female might have fed on the occupant within the last hour, but might equally well have fed elsewhere (perhaps at an earlier hour) thereafter entering the hut for shelter. Further, a short trial series of catches showed that mosquitos might enter or leave a hut either before sunset or after sunrise. Even then the full complexity of the movements of mosquitos in houses was not realised and it is only recently that a really authoritative review of this complicated subject has become available (Muirhead Thomson, 1951*b*). It thus became obvious that catches must be made of mosquitos actually biting and further, that though a particular species might be classed broadly as crepuscular, nocturnal or diurnal, catches which covered a part only of the 24-hour cycle could not be relied on to give a complete picture of its biting-activity. Plans were accordingly made for a series of catches in which the mosquitos biting the occupant of a hut would be collected by one worker, while another would collect those which entered the hut and settled without biting. These catches were planned to cover complete 24-hour periods. Unfortunately, shortage of time and administrative difficulties did not permit this work to be begun at Kisumu. At that time, of course, the window-trap designed by Muirhead Thomson (1948) was not yet available. Since its introduction it seems to provide, in many ways, information equivalent to that obtained by night catches, except with reference to the actual act of biting and, in elucidating the complicated behaviour of mosquitos in houses, it seems to have many advantages over ordinary catching.

Early in 1942 the writer began work on mosquitos in Uganda, in relation to field studies on the epidemiology of yellow fever. This work, which was almost exclusively concerned with species found in banana plantations and in rain-forest, gave an opportunity for trial of the 24-hour method. During 1942 and 1943 thirty such catches were made, 15 in forest and 15 in banana plantations. The catches were made at ground-level in various localities in Bwamba County, Toro District, and were carried out by units of varying size, dependent on the availability of staff. The results of this first study (Haddow, 1945*a*) were productive of much new information, and clearly emphasised the necessity for basing conclusions on standardised catches covering complete 24-hour periods. As an example of the type of fallacy which may arise from studying a part only of the 24-hour cycle, the case of *Eretmapodites chrysogaster* may be mentioned. It was known that this species will bite man readily under laboratory conditions (Bauer, 1928). On the basis of his night-catches, however, Kerr (1933) concluded that this is not the case in nature. The first series of 24-hour catches in Bwamba at once explained this difference in results, as it was shown that *E. chrysogaster* is almost exclusively diurnal, and so had not been picked up in Kerr's night catches. Indeed, one of the most suggestive general observations made during this first series was that a surprisingly large number of species are diurnal or mainly so.

The first series were carried out by experienced African catchers working on baits of African boys. As work at Kisumu had shown that the attractiveness of washed and unwashed baits was quite different, and further that female mosquitos could be induced to enter an otherwise empty hut in fair numbers by baiting it with dirty clothing, these variables were eliminated in the present series by having all the baits bathed before the catch and by removing their clothes to some distance from the catching-point. Further, as at Kisumu it had been found that the number of mosquitos entering a hut increased with increase in the number of occupants, the tendency in these first catches was to use the largest number of boys available. Concurrent routine work, however, showed that this factor did not apply to anything like the same extent in the open air, and it became obvious that small baits could be used, an important consideration in view of the high general cost of this type of work.

The first catches overcame by gradual education the unwillingness of the Africans to work outside by night. Their fears were easily understandable in an area such as Bwamba where the forest abounds with dangerous game. Superstitious fears, however, were more difficult to overcome and for long continued to give trouble. The inclusion in the first series, however, of a locality regarded with superstitious dread went far to overcome these fears, as the team concerned returned in full health after spending the night there. While this risk proved worth while, it is to be recognised that any illness or accident on the night concerned might have had serious consequences as far as the future of the investigation was concerned.

As staff became trained, it was decided that the baits themselves would act as catchers, the senior African staff being released for supervisory duties. It was further decided that, whenever possible, the catches would be made in series of several days and nights at a time. As it had been found that individual Africans might vary considerably in their attractiveness for mosquitos, it was clearly unsound to allow a whole unit to go off duty at one time to be replaced by another. Instead, a staggered shift system, discussed below, was introduced. This method finally allowed as many as six catches to be carried out in one operation, as the work itself is anything but strenuous. It was also realised that the teams were more interested in their comfort than in the extra pay which they received for night work, and it became fixed policy to provide abundant supplies of food and tea, tents for resting in (at some little distance from the catch) and a whole-time cook.

By this time it had been found that immunity to yellow fever was widespread among the monkeys of the Bwamba lowlands, and further, that it was prevalent among certain species which rarely descend to ground-level (Haddow & others, 1947b). The implication was that the disease among monkeys was being transmitted by an Arthropod which was arboreal in its biting-habits, as in South America (Bugher & others, 1944). Accordingly, it was decided that the arboreal mosquito fauna, if any, should be sampled by means of 24-hour catches with controls at ground-level. The local Africans, however, were far from willing to undertake this work as, though members of a forest tribe, they are poor climbers. Two short trial catches were, however, made by day, and in one of these two *Aëdes apicoargenteus* were taken at about twenty feet above ground. Having obtained this indication, it was decided that the work must go on and that the soundest approach would be to train the boys to work on very low platforms before attempting to sample the fauna of the main canopy. In this connection it was felt that further studies should be made on *A. simpsoni*, a mosquito prevalent in banana plantations, from which yellow fever virus had been isolated in 1941 (Mahaffy & others, 1942) and again in 1942 (Smithburn & Haddow, 1946). A group of platforms was therefore built in a banana plantation at heights of 6, 12 and 18 feet, and on these a series of ten catches was carried out simultaneously at each level, with a ground-level control. Each unit in this series consisted of four catchers (with reserves). The work yielded a good deal of information about *A. simpsoni*, which was found to be quite prevalent up to the highest level sampled (Haddow, 1945*b*), and at the same time accustomed the staff to the idea of work on platforms.

In April 1944, towards the end of this series, yellow fever virus was isolated from a mixed group of *Aëdes* spp. taken in uninhabited rain-forest at Mongiro, some miles away (Smithburn & Haddow, 1946). As it was already known that the monkeys of this area showed a high incidence of immunity to yellow fever, work in trees was obviously required urgently, and preparations were at once begun. Thanks to the Directors of Medical Services of the Uganda Protectorate and of Kenya Colony, Messrs. J. D. Gillett and R. B. Highton were seconded to take part in the work, and with their help the investigation was enabled to go forward rapidly. Platforms were built at Mongiro at 16, 31 and 54 feet, and in the adjacent forest area of Mamirimiri at 22, 44, 58 and 82 feet. With three Europeans and a much augmented African staff, ten 24-hour catches were carried out at Mongiro and ten at Mamirimiri. In these catches, which were completed during the main rains, units of four boys were again used, catching simultaneously at each level and with a control at ground-level. Though yellow fever virus was not isolated again at that time, a large amount of new information was gained, and now for the first time the full complexity of mosquito biting-behaviour began to be appreciated. Thus it was found that some species were most prevalent in the canopy, others in the understorey, and others at ground-level. Further, in the case of a particular level, the different species succeeded one another in their time of principal biting-activity. The writer made a second series of ten catches at Mongiro and ten at Mamirimiri in the dry weather of early 1945. These were exactly comparable to the earlier series, and the same platforms were used. These later catches showed that certain changes in vertical distribution might be induced by seasonal alterations in weather (Haddow & others, 1947*a*).

The main results of the work outlined above have already been published in the papers quoted. The following data and analyses, however, including very much more extensive series, have not as yet been published.

It had been found as early as 1943 that yellow fever was prevalent among monkeys in the Entebbe area (Haddow & others, 1951) and for this reason work in that neighbourhood was begun, though not until 1946, two small forest areas within a few miles of this Institute being chosen. In the first of these (Kitinda) a platform was built in the canopy and one at understorey level in the same tree. In the second area (Zika) six similar sets of platforms were built, in each case the canopy and understorey platforms being built in the same tree. The canopy platforms ranged from 52 to 65 feet, with a mean of 57 feet, and the understorey platforms from 27 to 38 feet, with a mean of 35 feet. At the same time no fewer than forty canopy platforms were built in Bwamba, covering a long stretch of the edge of the Semliki forest. These were built in forest of all kinds, and their heights ranged from 36 to 77 feet (with a mean of 54 feet), though all were in the main canopy of their own particular areas. Unfortunately, it was not possible to build corresponding understorey platforms, on account of time restrictions and the high cost of the work.

These platforms were built primarily to accommodate susceptible rhesus "sentinel" monkeys, in the hope that illness among these might reveal a focus of virus activity. They presented, however, an excellent opportunity for an extensive survey of the arboreal mosquitos in forest of many different types and at many different levels above ground. Accordingly, during the period 1946–48 series of catches were conducted on all of them, with controls at ground-level, these surveys being named the "Bwamba Tree Survey" and the "Entebbe Tree Survey" respectively. The details were as follows: In the Entebbe survey each series consisted of five 24-hour catches, with three boys on the canopy platform, three on the understorey platform, and three at ground-level. There were thus 35 catches (5 catches on 7 trees, see above) in the survey, and in addition five were made at ground-level in a banana plantation, abutting on the forest at Zika, and five in a hut 80 yards from the forest edge, the bait in both cases consisting of three boys. In the Bwamba survey each series consisted of six catches, with three boys on the platform and three at ground-level. During 1947–48, as the work was nearing completion, an arboreal mosquito, *A. africanus*, was finally incriminated as a forest vector of yellow fever (Haddow & others, 1948; Smithburn & others, 1949). It is interesting to note that, largely as a result of information gained from 24-hour catches and from the study of immunity among wild monkeys, it had been possible to incriminate this species on purely theoretical grounds as early as 1944, four years previously (Smithburn & Haddow, 1946).

The foregoing summarises the various series of 24-hour catches made to date by the author, with human bait. Some catches have also been made by similar methods, but with anaesthetised monkeys as bait (Haddow & Dick, 1948). It should be mentioned that Tabanids occurred fairly frequently in the canopy, but the results for these insects have already been reported in detail (Haddow & others, 1950; Haddow, 1952). The sample of mosquitos taken in these various series is very large. Thus the writer's collections of adult African mosquitos totalled 384,282 specimens at the end of 1951, and of these 107,567 have been taken in 24-hour catches. The number of species and groups encountered in these catches so far is 84. The general results are shown in Table I.

The technique, difficulties and interpretation of results may now be discussed, but mention must first be made of the studies of other workers in this field.

The 24-hour method has been extensively employed—so far as the author is aware—only by the Yellow Fever Research Institute (now the Virus Research Institute), Entebbe, and by the kindred Institute at Lagos, Nigeria. Thus, Dr. W. H. R. Lumsden carried out informative series in Bwamba during 1947–48, in which catches were carried out simultaneously in closely adjoining but otherwise dissimilar environments, namely a hut, open ground, a banana plantation, the forest floor and the forest canopy (Lumsden, 1951). He also carried out series in which arboreal units worked in conjunction with ground-level controls in West Nile District, Uganda (Lumsden & Buxton, 1951), and at Gede and Taveta in the Coast Province, Kenya (in press). In Nigeria, Mattingly carried out valuable series in forest during 1945–46, using units at four levels, with a ground-level control (Mattingly, 1949*a*,*b*). Mattingly's work has proved of particular interest as it has shown that in the case of species common to Nigeria and to Uganda the biting-cycle and vertical distribution are usually similar in both countries. Finally, Gillett (1951) has carried out series designed to elucidate the behaviour of *A. simpsoni* in various parts of Uganda. It is understood that the 24-hour method has recently come into use in Kenya, but nothing has so far been published from that country.

TABLE I.

Summarised results of the writer's various series of 24-hour catches, to date.

Date	Locality	Environment	No. of catches	No. of levels	Size of units	Total man-hours	Total mosquitos
1942–43	Bwamba	Forest	15	1	5–10	3,312	2,185
1942–43	"	Banana pl.	15	1	10–16	4,824	1,852
1943–44	"	"	10	4	4	3,840	687
1944	"	Forest	10	4	4	3,840	10,507
1944	"	"	10	5	4	4,800	8,969
1945	"	"	10	4	4	3,840	7,219
1945	"	"	10	5	4	4,800	5,820
1946–48	"	"	240	2	3	34,560	40,671
1946–48	Entebbe	"	35	3	3	7,560	24,240
1948	"	Banana pl.	5	1	3	360	3,528
1948	"	Hut	5	1	3	360	1,889
Totals			365	—	—	72,096	107,567

In South America there has not been, so far as the author is aware, any 24-hour work closely comparable to that carried out in Africa, though Kumm and Novis (1938) and Bates (1944*a*) have carried out day catches and Davis (1944) has made interesting 24-hour catches with birds as bait. Davis used trap-nets of the Shannon type, the mosquitos being removed from them every hour.

The Numerical Size of the Baits and the General Conduct of Catches.

As mentioned above, work in Bwamba was begun with numerically large baits, but it was found subsequently that small units were equally satisfactory. In all the later catches, for reasons which will be discussed below, three boys formed a unit, and the writer considers this to be the ideal number.

Owing to the fact that individuals differ in attractiveness, one entire unit should not be exchanged for another during a catch. Instead, a staggered shift system is used, one boy going off duty each hour, to be replaced by another who has been resting. Thus, when units of four are used, the shortest spell of duty must be four hours, and this has been found to be rather tiring. With a unit of three and a spell of three hours the results have been more satisfactory. A further point is that in the case of a unit of three the platform can be quite small and light.

With regard to the numbers in the reserves, various points may be noted. At first large reserves were used to permit long rest-periods. In spite of this the Africans, with their almost insatiable capacity for sleep, still tended to fall asleep on the platforms. This problem gave much trouble and was not easily solved. At one stage benzedrine was tried, but it proved to be less effective in Africans than in Europeans. The difficulty was finally overcome by ruling that only one boy at a time was to catch actively, using himself and the other two as bait. Of course if a mosquito were to bite, say, the middle of his back, he could call on them for assistance, but essentially they were considered as baits only. Thus they could sit or, if they so desired, lie down and go to sleep. The catcher had to remain on his feet and prove his wakefulness by responding at once to frequent hails and questions from the supervisor. This method permitted considerable reduction in the number of reserve catchers, and finally the unit employed was five—three working and two off duty. The system was that each boy acted as catcher for the first hour after coming on duty. He then had two hours' light work, followed by two hours' rest. With such units continuous series of five to six catches were easily achieved.

In view of personal differences in attractiveness and also in skill, it is desirable that a given individual should not be employed at exactly the same periods each day. For this reason again the unit recommended above is suitable, as on each successive day a particular catcher's duty periods begin one hour later. If, further, the series consists of five consecutive 24-hour catches, the arrangement is almost ideal. Thus, as is shown in Table II, at the end of the series each member of the team has caught once, has acted as bait twice, and has been off duty twice at each hour of the twenty-four. This was the method used in the Entebbe Tree Survey, the most satisfactory series of catches so far carried out by the writer.

TABLE II.

Spells of duty of each mosquito catcher in a unit of three with two reserves, carrying out a continuous series of five 24-hour catches.

Period	1	2	3	4	5
06–07	*	·	·	o	o
07–08	o	*	·	·	o
08–09	o	o	*	·	·
09–10	·	o	o	*	·
10–11	·	·	o	o	*
11–12	*	·	·	o	o
12–13	o	*	·	·	o
13–14	o	o	*	·	·
14–15	·	o	o	*	·
15–16	·	·	o	o	*
16–17	*	·	·	o	o
17–18	o	*	·	·	o
18–19	o	o	*	·	·
19–20	·	o	o	*	·
20–21	·	·	o	o	*
21–22	*	·	·	o	o
22–23	o	*	·	·	o
23–24	o	o	*	·	·
00–01	·	o	o	*	·
01–02	·	·	o	o	*
02–03	*	·	·	o	o
03–04	o	*	·	·	o
04–05	o	o	*	·	·
05–06	·	o	o	*	·

One man goes off duty each hour, in rotation. Key to signs: *, on duty; °, on light duty; ·, off duty.

In South America (Bates, 1944*a*) and in West Africa (Mattingly, 1949*a*,*b*) pairs of workers were the rule. This method, however, has the disadvantage that both must remain awake and alert. Further, if a shift system is to be used, there is a danger that differences in attractiveness and catching-skill may be sufficiently pronounced to affect the results in the case of so small a unit.

Even using small groups such as are advised above, the staff required is considerable. There are the catchers, the cook, and the supervisors. There should be not less than two supervisors, and three is the number to be aimed at. In addition there should be one, or preferably two spare catchers, especially in wet weather when malaria is prevalent. Thus, in the case of a series carried out at three levels, the team would be: *Supervisors*, 2 or 3; *Canopy unit*, 5; *Understorey unit*, 5; *Ground-level unit*, 5; *Reserve catchers*, 1 or 2; *Cook*, 1; *Total*, 19 to 21. It is thus hardly surprising that costs are high, as in addition to the salaries of the team (probably augmented on account of night work) there is the cost of food and transport. It may be objected that, if single catches of 24 hours each were to be made, the reserves and rest periods could be dispensed with, the total team thus being reduced to 12, who would work throughout the catch and rest the next day. In practice, however, this is not economical, as the method is exhausting to the staff and also to the European in charge, who must pack and check all the apparatus, food, etc., for each individual catch. Transport costs are also increased.

Points which require constant attention from the supervisor are as follows: Smoke from the cook's fire must be carefully watched. No amount of mere telling will convince the teams that if it drifts through the catching-area the results may be affected, and even after years it will be found that the catchers have not grasped the quantitative and comparative nature of the work. Even more important than this is the point that the undergrowth must be disturbed as little as possible. No matter what the usual periodicity of a mosquito, it may bite at any time of the day or night if the vegetation is agitated. Tents should not be too close to the catching-point, and smoking should be permitted at the tents only. Finally, light tarpaulins should be rigged at some height over the catchers. These do not seem to affect the result, and once begun, a catch must be carried on no matter how bad the weather may become.

Catching and Sorting Procedure.

After trying various methods, it became obvious that the only satisfactory one was to catch each mosquito separately in a tube, plugging this with cotton wool. Only by this method can large catches be sorted rapidly, if, as in most virus work, the mosquitos are required alive afterwards. A short tube is desirable if the mosquitos are to be released into cages, and it should be narrow enough to permit a hand-lens to be focussed on the far side. Round-bottomed tubes 15 × 85 mm. have been found excellent. Flat-bottomed tubes are much more fragile and plastic tubes, though free from this disadvantage, are less transparent and soon become scratched.

Wire racks designed to hold large numbers of tubes vertically are a great help in sorting. Where numbers are large, 1,000 mosquitos or over, a preliminary sorting into genera and a few of the commonest species is made, after which a more detailed examination follows. The preliminary sorting can often be done largely with the naked eye. The most useful lenses are aplanatic " triplets " of low power with a magnification of 6× or 7×. The use of higher powers greatly reduces the working distance, the size of the field and the brilliance of the image. In any case, a mosquito which cannot be identified with a magnification of 6× or 7× will almost certainly call for the use of a low-power microscope.

Each hour's catch is placed in a separate bag on which the level and a serial number are marked clearly. Tie-on labels are not suitable as they are easily lost, particularly in wet weather. Where possible, the different levels should have bags of different colours. At first the bags were marked by hour and level, but this was found to be confusing as Africans do not readily become accustomed to the 24-hour clock, and particularly as the catches might be begun at any hour. During most of the work, therefore, the bags were simply numbered from 1–24.

One of the main duties of the supervisor is to hand out and receive bags, checking the numbers and levels. The present system for platforms is that the catcher coming off duty brings down the bag with the last hour's catch, while the catcher going up takes with him the new bag and a supply of empty tubes.

The number of bags and tubes required is, of course, considerable. Thus, for a single 24-hour catch at three levels, 72 bags will be required, and where catches are to run continuously this number should be doubled, so that one catch may be sorted while the next is in progress. As far as tubes are concerned, individual catches in certain areas have quite frequently yielded over 1,000 specimens (from the results in Table I it will be seen that the mean catch per level per day is almost 130 mosquitos). In addition, the breakage-rate of tubes is always high.

Mosquitos are caught as they land to bite, and those alighting on the platform or the vegetation are ignored. In spite of this it will be found that the catches include a certain number of males and of species not known to bite man (some *Uranotaenia* spp., for example). The reasons are not clearly understood, but it may be that such mosquitos are alighting to suck sweat, perhaps in order to obtain salts.

The writer feels that for most purposes hand-catching is to be preferred to the use of trap-nets or trap-cages. Thus, at Kisumu in 1940–41, he made trial catches with trap-nets of different forms but did not find them satisfactory, and at Entebbe and in Bwamba further trials with nets of various designs based on the Shannon trap (Shannon, 1939) confirmed this result. The experiments led to the conclusion that unless mosquitos were caught continuously inside the trap many would certainly escape, and the traps had thus no advantage over fully-exposed baits. Further, it was shown that more mosquitos were attracted to an exposed bait than to one inside a trap (Haddow, 1945*a*). In the case of catches made on animals a possible fallacy was introduced by the presence of a human catcher, but this could not have been eliminated by the use of a trap-net, as continuous catching would still have been necessary unless many mosquitos were to be lost. It is not doubted that in the case of very large animals such as goats or donkeys the stable-traps described by Magoon (1935) and Bates (1944*b*) have in some areas proved most useful. In the heavy forest conditions under which most of the present work was carried out, however, they would have been most unwieldy, and in the case of work in the canopy, quite impossible to use.

It is further to be remembered that while some mosquitos readily enter the small openings of traps, not all will do so. Thus it was found that, while *A. africanus* readily bites monkeys of various species in the open (Haddow & Dick, 1948), it will not enter "sentinel" cages to do so, and these cages had to be discarded for this reason (Haddow & others, 1948). In these cages, the entire floor and most of the front was made of expanded metal with a wide mesh, either 1 × 3 inches or $1\frac{1}{2}$ × 4 inches. Had our field work been based on trap catches, it is highly unlikely that *A. africanus* would yet have been incriminated as a vector of yellow fever, and it is also unlikely that its prevalence would have been recognised, unless by the notoriously unreliable method of larva surveys.

The main feature of the trap method is that light is dispensed with except at the collection periods, but in any type where continuous catching is necessary this advantage is of course lost. While the use of lights must certainly introduce an error (especially in the case of genera such as *Taeniorhynchus*, which are attracted by light) the distortion of the results is probably less than in the case of an hourly catch in a trap-net, where there is certainly a considerable loss of the mosquitos which have entered the net and where, on the other hand, there is no certainty that the mosquitos which are obtained have entered to bite. These difficulties have not been overcome, but they have been minimised by the use of the lowest light intensities which will permit the mosquitos to be seen. At first electric hand-torches were used, the light being dimmed and diffused by several thicknesses of white cloth over the glass. Later, owing to the difficulties of maintaining supplies of batteries, hurricane lamps came into use, these being employed with the flame well turned down. Although on the whole these lamps were satisfactory, their life in African hands is exceedingly short. Another disadvantage is that the glasses, when hot, tend to crack in rain, or even when brought into contact with wet foliage.

Recently, Johnson (1950*a*,*b*, 1951) has had marked success in the use of suction-traps for small airborne insects, these traps being designed to segregate each hour's catch automatically. A colleague, Dr. W. H. R. Lumsden, using a different type of suction-trap, has carried out a first investigation by this method in rain-forest in Uganda. His results (in preparation) indicate that, although many difficulties remain to be overcome, the method has great future potentialities. The principal advantage of this method is that if the trap is unbaited and unlighted it gives a sample of the flying mosquito population, and not merely of that section of the female population which is conditioned for biting at the time concerned.

Timing and Time-Intervals.

Accurate timing is naturally a most important part of the work. Usually cheap and easily replaced alarm clocks were used, but it is now felt that this was not the best approach to the matter, as they constantly required repair or replacement. A better method would have been to provide 8-day clocks (which run for longer than the duration of even the most extended catch) mounted in locked boxes with glass fronts, and set at headquarters before the beginning of the work.

All the earlier catches were carried out by Local Mean Time (L.M.T.), *i.e.*, Greenwich Mean Time with a correction for longtitude. A colleague (Dr. W. H. R. Lumsden) has, however, pointed out that this system represents only an approximation to actual sun time. Thus, at the equator, its use might introduce an error of as much as + 18 or − 13 minutes at certain times of the year, though in general it would be much less. In higher latitudes the error might be considerable.

In mosquito studies the time of sunset is very important, as various species of biting Diptera show a sudden wave of activity just at dusk. This may, as in *A. africanus*, represent the main biting-peak or, as in *Anopheles gambiae*, a minor peak. In view of the error introduced by the use of L.M.T., it was at first thought that some of the writer's results for the sunset period might be seriously affected, as a biting-period at the beginning of the hour following sunset might be attributed to the preceding hour. Fortunately, however, in the case of the species so far studied, the main wave does not occur till 20 minutes after sunset or a little later (Lumsden, 1952) and 20 minutes exceeds the maximum possible error. Further, it so happens that the great majority of the catches were carried out at times of year when the error is in any case small. If, however, the author's work had been carried out at any great distance from the equator, the error would have been increased in some series, and the results might have been seriously vitiated.

With regard to the time-intervals into which the catch is to be divided, the author wishes to emphasise that they should be as short as is compatible with the administration of the work in the field, more particularly as it is always possible to regroup short periods into longer ones. Throughout the work the period used has been one hour, but recent studies by Lumsden (1952) have shown that, in the case of certain species, even shorter intervals are desirable. For example, it was known that the main biting-activity of *Aëdes africanus* was confined to the hour after sunset, but Lumsden's observations have shown that the main wave occupies only about 20 minutes, a point of considerable interest. Thus, generally speaking, it is felt that the chosen period should be a short one, and in this respect it is felt that one hour is probably the longest permissible.

As at the equator the relative lengths of day and night vary very little throughout the year, it is possible to compare the results of catches made at different seasons on the basis of fixed time-units. In higher latitudes, however, the seasonal variations in the duration of day and night preclude the use of such a method, and in such cases the only answer would seem to be the system introduced by C. B. Williams (1939) who, in analysing the results of light-trap catches, divides the whole period between dusk and dawn into a fixed number of units (eight) regardless of their actual duration.

The time at which 24-hour catches should be begun should ideally be the same always. In practice, however, this is frequently not possible. Transport difficulties, to give only a single example, may delay the arrival of a unit at the catching-station. The cost of maintaining units in the field being high, it is not economically feasible to keep them waiting until the next time that the chosen hour comes round. Thus in practice they must begin catching at the next clock-hour after their arrival. It is to be emphasised, in any case, that the whole system of 24-hour catching is based on the concept of a biting-cycle (Haddow, 1945*a*). Broadly speaking, the view advanced is that the biting-behaviour of a given species will, on successive days, follow roughly the same pattern so far as time is concerned. Some species show quite remarkable regularity in this respect though others, it must be admitted, are rather irregular. Thus, for practical purposes the 24-hour period must be regarded as a closed cycle within which biting-behaviour will be repetitive, and which can therefore be entered at any point which is convenient, so long as the catch is thereafter prolonged for 24 hours or multiples of 24 hours. An illustrative example is given in Table III. Here three forest-canopy catches of *A. africanus* are shown for comparison. They were made in different years, in different months, and at different stations (one of which was about 200 miles from the other two). The levels were all different, though all the stations were in the main forest canopy of their particular locality. The starting-times were all different (12 hours, 14 hours and 17 hours). In two cases the catch was made at canopy-level with a control at ground-level, but in the third (Zika II) there was also a unit in the understorey. In spite of these manifold differences, it is obvious that the picture of biting-activity was essentially the same in all three catches, and there seems to be no reason why the results should not be combined.

Time-Intervals and Interpretation of the Biting-Cycle.

It has been mentioned above that in making the catch the time subdivisions of the 24 hours should be short. It remains to discuss the grouping to be employed in interpreting the results.

In earlier papers, while the sample was small and experience limited, the author used a four-hour grouping of the results, except in the cases of one or two of the most abundant or most important species (Haddow, 1945*a*; Haddow & others, 1947*a*). The grouping selected was one which corresponded approximately to the main microclimatic phases of the 24-hour period, namely, 06–10, 10–14, 14–18, 18–22, 22–02 and 02–06 hours. As far as they went these results were useful in indicating general trends. With increasing experience, however, it has become apparent that the smoothing of the curves resulting from the use of wide groupings does not compensate for the loss of detail and further, that false impressions may be produced, both of the activity of the mosquito and of the dependence of its biting-cycle on extraneous factors such as microclimate. The latter point will be discussed in a separate section.

TABLE III.

Comparison between three 24-hour catches of *Aëdes africanus* in the forest canopy.

Hours, L.M.T.	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	Total
Catch begun at 17 hours, at Zika II, 52 feet, 26–27 July 1946	4	—	—	—	—	—	—	—	—	—	—	1	24	6	3	1	3	2	1	1	—	—	1	—	47
Catch begun at 14 hours, at Mamirimiri, 64 feet, 12–13 December 1947	2	—	—	—	—	—	—	—	—	—	—	1	16	6	2	6	2	2	—	—	—	—	—	3	40
Catch begun at 12 hours, at Mongiro IV, 58 feet, 15–16 June 1948	—	—	1	—	—	—	—	—	—	1	—	—	12	9	5	3	—	—	—	1	1	—	—	—	33
Combined result	6	—	1	—	—	—	—	—	—	1	—	2	52	21	10	10	5	4	1	2	1	—	1	3	120

TABLE IV.

The biting-cycle of *Anopheles coustani* var. *ziemanni*, at ground-level, Entebbe area.

Hour	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	
Hourly totals .. .. As percentage	— —	— —	— —	— —	— —	— —	— —	4 7·7	6 11·5	5 9·6	7 13·4	6 11·5	4 7·7	3 5·8	3 5·8	5 9·6	2 3·8	5 9·6	1 1·9	— —	1 1·9	— —	— —	— —	52
Two-hourly totals .. .. As percentage	— —		— —		— —		4 7·7		11 21·2		13 25·0		7 13·4		8 15·4		7 13·4		1 1·9		1 1·9		— —		52
Three-hourly totals .. As percentage	— —			— —			10 19·2			18 34·6			10 19·2			12 23·1			2 3·8			— —			52
Four-hourly totals.. .. As percentage	— —				4 7·7				24 46·1				15 28·8				8 15·4				1 1·9				52

In this example the starting-point for all groupings is 12 hours.

A further objection may be raised, namely that in the case of grouped results there will be a variety of curves possible dependent on the starting-point. Thus in the case of a 2-hour grouping there are two possible arrangements, depending on whether the starting-point is an odd or an even hour; in a three-hour grouping there will be three possible arrangements, and so on.

In the case of a mosquito with a biting-peak confined to a single hour, each of the four possible 4-hour groupings will show this peak at a different point in time, and similarly with the 3-hour and 2-hour groupings. Thus in the case of the figures given for *A. africanus* in Table III, 4-hour groupings would show the main biting peak as follows:—

(a) Grouping 06–10 hours, etc. The biting-peak appears in the period 18–22 hours, with a midpoint at 20 hours.

(b) Grouping 07–11, 11–15 hours, etc. The biting-peak appears in the period 15–19 hours, but the figure for 19–23 hours is also very high. The picture in this case is of a very wide peak. The midpoint of the highest period is at 17 hours.

(c) Grouping 08–12, 12–16 hours, etc. The biting-peak is in the period 16–20 hours, with a midpoint at 18 hours.

(d) Grouping 09–13, 13–17 hours, etc. The biting-peak is in the period 17–21 hours, with a midpoint at 19 hours.

Thus the midpoint of the peak period appears in these four groupings as at 17, 18, 19 and 20 hours. None of them show the true brevity of the wave, with its single clear-cut peak in the period 18–19 hours (or, more precisely, according to Lumsden, 1952, in the period 18.20–18.30 hours). Even when a finer 2-hour grouping is employed, the peak is centred either on 18 hours or on 19 hours, and the results thus "bracket" the true peak but do not indicate its position accurately.

These figures show how markedly the use of groupings may affect the results in the case of a very pronounced wave of biting-activity. In the case of minor peaks, the effect is to eliminate them almost completely. In the earlier stages of the investigation, the tendency was to regard these as being due to chance or to the small size of the sample, but the much more detailed analysis of large samples which is at present proceeding has shown that some at least are of regular occurrence and undoubted significance. Thus Lumsden, studying a small peak of biting-activity shown by *Anopheles gambiae* in the forest canopy in the hour after sunset, has been able to introduce an interesting theory to the effect that it may be due to a biting-wave consisting mainly of the older section of the population. Reviewing a long series of catches of *A. gambiae*, the writer finds that though his grouping is wider (on an hourly basis) this peak is shown clearly in the results, being sufficiently well marked to affect the results for the entire hour after sunset. It appears, however, only in that small section of the population which bites in the trees, and is not apparent in the much larger sample taken at ground-level. The problem thus increases in complexity. The great wave of biting-activity in the case of *A. gambiae* occurs in the latter part of the night, and is fairly well shown in coarsely-grouped results. These, however, tend to eliminate the minor fluctuations which follow sunset, and of which at least one may be important in interpreting behaviour.

Another objection to the grouping method is that it may give a very exaggerated view of the biting-pattern, and sometimes quite an erroneous one. In this connection it is interesting to review an actual case, a suitable example being the ground-level biting-cycle of *A. coustani* var. *ziemanni* in the Entebbe area. The sample is small, but has interesting characteristics in the present connection. As *A. coustani* var. *ziemanni* is nocturnal, midday is a convenient starting-point for the curves. The hourly figures (Table IV and fig. 1) show that biting is almost completely confined to the hours of darkness, and that at no point does it show a very pronounced peak. The impression is of a series of irregular waves, grouped vaguely into two main periods of biting-activity with an ill-defined phase of lower activity between. The highest point is reached in the period 22–23 hours. The general picture is a vague one, and clearly, on this sample, it would not be justifiable to say much more than that the mosquito is essentially nocturnal.

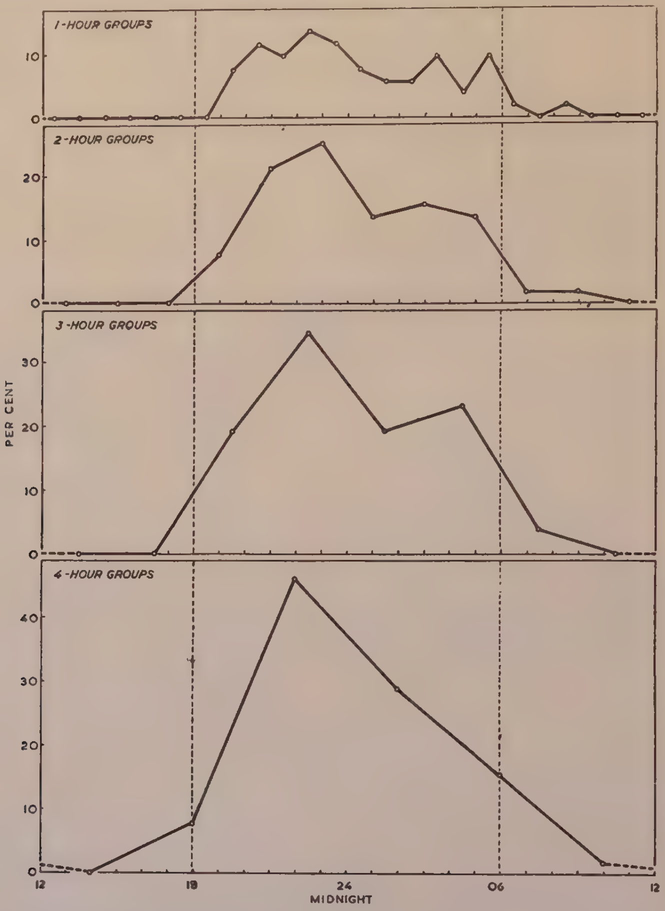


Fig. 1.—The biting-cycle of *Anopheles coustani* var. *ziemanni* at ground-level, in the Entebbe area, by 1-, 2-, 3- and 4-hour groupings.

When a 2-hour grouping is employed, the impression of a series of minor waves has already been lost. Further, the earlier wave—that before midnight—has become much exaggerated. The same characteristics are shown by a 3-hour grouping, but in a still more pronounced manner. In the 4-hour grouping, however, the impression is of a single massive wave of biting-activity, bearing little resemblance to the original figures. In this case the period after midnight, which is actually one of low activity, now appears higher than that before sunrise. Of course, these grouped results could be based on 2, 3 or 4 starting points respectively. For purposes of the present comparison, however, the starting point has been midday in each case. Thus the groups begin 12–14, 14–16 or 12–15, 15–18, or 12–16, 16–20, and so on. Another point of interest in the present example is that only in the 1-hour grouping is it clear that no *A. coustani* were taken until the second hour after sunset.

For long the writer held the view that groupings of very different lengths might be suitable for different mosquitos. Thus in the case of a species with a single short wave of intense activity such as *E. chrysogaster* or *Aëdes africanus*, a very short period would be desirable. In the case, however, of species whose biting-activity was spread over many hours, it seemed that a wide grouping might not only show the trend more clearly, but might actually give a truer picture of the behaviour. It was felt, in fact, that in the case of certain species consistent behaviour could only be shown by a coarse grouping, and further, that such mosquitos really "behaved by long periods." The fallacy is of course that these are just the species whose behaviour is the least consistent and repetitive. Experience thus having failed to support the earlier view, the writer has abandoned it and is now convinced that a 1-hour grouping is the widest permissible, except perhaps in cases where the sample is very small. It is in any case doubtful whether small samples are of much value in appraising biting-habits, except where no further work can be contemplated.

Main Types of Biting-Behaviour.

Broadly speaking, mosquitos may be divided into two main classes where biting-behaviour is concerned.

In the first group there is, at some time during the 24 hours, a single, short, very pronounced wave of biting-activity, such activity being of minor degree at all other times. A subtype of this kind of behaviour is that in which two such waves occur, usually at sunset and dawn. The best example of this type so far found among mosquitos is that of *A. irritans* as noted by Mattingly (1949*b*), though among other insects a very clear-cut case of a slightly different type has recently been described for a Tabanid, *Haematopota nefanda* Edw. (Haddow, 1952). It must be remembered, however, that even in cases where there is a single clear-cut wave, biting is never completely confined to the period concerned. Thus *A. africanus* bites throughout the 24 hours, but a very large proportion of the total will usually be taken in the single hour after sunset.

The mosquitos belonging to this group show certain other characteristics in common. Thus they usually exhibit a marked preference for some particular level, as well as for a particular time. Another important point is that, with very few exceptions, they breed in small containers such as tree-holes, plant-axils, leaf-pools, crab-holes, domestic receptacles, etc. Among the exceptions the best example is *Aëdomyia africana*, as reported by Mattingly (1949*b*). These habits have no relation to systematic position and examples may be found in many genera, though it is only in a few groups such as *Eretmapodites* and *Stegomyia* that all members breed in small containers. Broadly speaking, therefore, mosquitos showing this type of biting-curve are specialised in their preference for a particular type of breeding-place, a particular time for biting and a particular level for biting. Some of these points have already been stressed by Haddow & others (1950) and by Lumsden (1952). Lumsden, discussing some nocturnal examples of this type of curve suggests that in these small-container breeders, in the case of which the total population is probably not very great, there is a necessity for long life with repeated ovarian cycles, and that much of the population will consist of females biting or laying for a second (or subsequent) time. His view is that during the hours of daylight these older females form an increasingly large group of mosquitos ready to feed but inhibited by light. Their release at sunset results in the single pronounced wave of biting-activity. Specimens coming to bite at later hours are considered to be young mosquitos, which were not ready to feed at sunset. This hypothesis of Lumsden's has much to recommend it in the case of *Aëdes africanus* and other species which bite in a similar way just after sunset, and indeed he advances it essentially to cover the behaviour of nocturnal mosquitos. Unfortunately, however, it does not seem to apply equally well in the case of the small-container breeders which bite by day. Applying Lumsden's argument the other way round, it might be supposed that in the case of the diurnal species the older group, inhibited by darkness, would build up during the night, and that a wave of activity would follow sunrise. The writer does not, however, know of any such case. Thus *A. simpsoni*, in localities where it is abundant, bites without interruption throughout the day, with only a slight slackening during the hotter hours. When it does show a preference this usually appears to be for the afternoon rather than the morning. Much the same may be said of *A. dendrophilus*. Among mosquitos showing a single very marked wave of activity, a good example is *A. apicoargenteus*, which bites throughout the day, but which reaches a very marked peak just before midday, *i.e.*, several hours after biting has started. Finally the case of *E. chrysogaster* may be mentioned. This species bites with a fair degree of freedom throughout the hours of daylight, but shows a major wave of activity just before sunset, *i.e.*, just before it ceases to bite. Its biting-curve (Table V and fig. 2) is therefore almost a mirror-image of that of *A. africanus*. In this Table the geometric mean (M_G) as used by Williams (1937, 1939) and multiplied by 100 has been used, for reasons which will be explained in the next section.

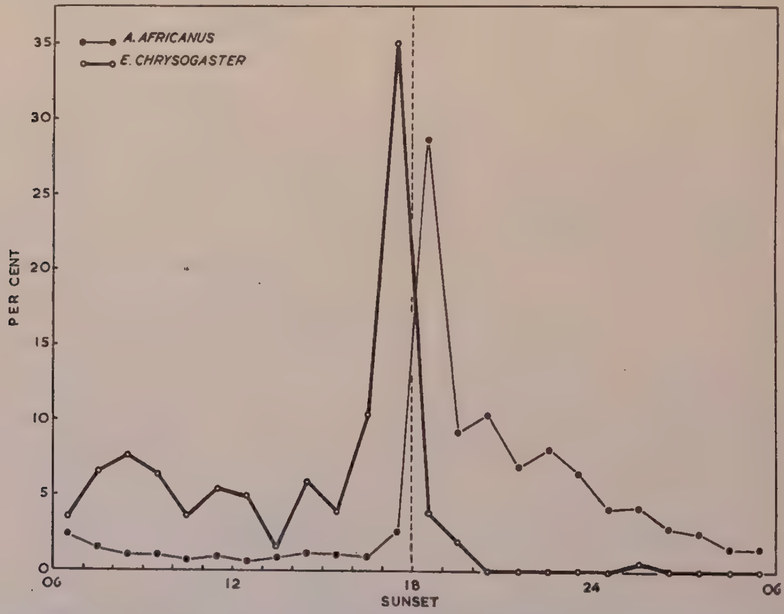


Fig. 2.—The biting-cycle of *Eretmapodites chrysogaster* at ground-level and of *Aëdes africanus* in the forest canopy at Zika, as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison.

It thus becomes apparent that a single explanation can hardly fit all these cases, though all the species mentioned are small-container breeders. There is one diurnal species, *A. longipalpis*, where Lumsden's hypothesis seems to fit the case closely. Detailed analysis of the activity of this species, which will be discussed further below, leads to the belief that biting is usually initiated by a fixed section of the population which may well be an age-group. At the moment there are no dissections available to give final proof.

In the other main group of species, the phase of active biting is prolonged.

TABLE V.

The biting-cycle of *E. chrysogaster* at ground-level and of *Aëdes africanus* in the canopy in forest at Zika.

Hour	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	Total
E. chrysogaster Total	6	10	13	12	7	10	8	3	11	8	17	50	6	3	—	—	—	—	—	1	—	—	—	—	165
100 M_G	14	26	30	25	14	21	19	6	23	15	41	139	15	7	—	—	—	—	—	2	—	—	—	—	—
M_G as percentage ..	3·5	6·5	7·6	6·3	3·5	5·3	4·8	1·5	5·8	3·8	10·3	35·0	3·8	1·8	—	—	—	—	—	0·5	—	—	—	—	—
A. africanus Total	24	14	14	11	8	8	5	8	12	10	9	45	279	116	95	69	76	58	39	41	26	21	15	15	1018
100 M_G	48	32	21	20	13	16	10	15	23	20	16	55	601	194	216	142	171	137	86	88	59	53	32	32	—
M_G as percentage ..	2·3	1·5	1·0	1·0	0·6	0·8	0·5	0·7	1·1	1·0	0·8	2·6	28·6	9·2	10·3	6·8	8·1	6·5	4·1	4·2	2·8	2·5	1·5	1·5	—

TABLE VI.

Twelve individual catches of *T. africanus* at ground-level, to show that the numerically highest catch may be taken at any hour of the night.

Hour	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	Total	Peak hour	
Catch No. B/258 ..	—	—	1	—	—	—	**42**	35	10	4	5	3	1	1	5	4	6	4	1	2	3	—	1	—	128	18/19	A
E/25 ..	1	1	—	2	1	—	7	**36**	11	6	7	8	10	8	4	10	4	9	5	8	3	—	2	1	144	19/20	
E/36 ..	—	—	—	—	—	2	9	20	**37**	21	18	16	16	12	13	13	3	7	4	3	1	1	—	—	196	20/21	
E/37 ..	—	—	—	1	5	3	2	5	9	**28**	14	23	23	11	9	13	14	17	7	2	2	—	1	—	189	21/22	
E/28 ..	1	—	1	1	—	1	17	10	24	15	**40**	11	14	9	12	19	12	11	9	2	—	5	—	2	216	22/23	B
E/23 ..	—	5	—	2	1	1	6	6	12	24	21	**32**	4	14	3	2	3	16	3	4	1	9	—	1	170	23/24	
E/34 ..	—	—	1	—	1	3	19	21	29	23	15	28	**42**	37	38	14	17	12	9	2	2	1	—	—	314	00/01	
B/255 ..	—	—	—	—	—	—	12	1	1	3	5	6	3	**13**	5	10	3	2	2	—	—	—	1	—	67	01/02	
E/44 ..	—	—	—	—	—	—	1	1	—	4	22	8	11	16	**64**	15	12	8	2	2	1	1	—	—	168	02/03	C
E/43 ..	—	—	—	—	—	—	4	2	1	16	24	32	40	10	30	**43**	37	9	6	4	—	3	1	—	262	03/04	
E/41 ..	7	5	1	3	4	18	15	24	8	22	34	30	42	53	34	130	**157**	39	9	8	9	10	7	3	672	04/05	
B/262 ..	—	—	—	—	—	—	1	3	1	5	2	—	—	1	2	2	1	**18**	2	1	—	—	—	—	39	05/06	

It may be, generally speaking, either nocturnal or diurnal, and in a few cases it may continue at a fairly high degree of activity throughout the 24 hours. Coupled with this is the fact that, while some time may be the most favoured, the biting-cycle is usually strikingly irregular. Thus in the case of *Anopheles gambiae* the latter half of the night and particularly the period before sunrise is the time of maximum biting-activity, but the comparison of individual nights will show very marked differences and even (in individual cases) complete reversal of the usual nocturnal periodicity. The biting-cycle differs, in fact, every night, at least as far as detail is concerned. A very good example is that of *Taeniorhynchus africanus*. Here, as is shown in Table VI, the biting-peak may occur at any time during the night. This example is rendered more striking when the following facts are considered. In the Entebbe area only 45 catches were carried out, yet, from this fairly short series, it was possible to select examples in which the peak had occurred in no less than nine of the twelve hours of darkness. For the remaining three it was necessary to consult the more extensive Bwamba series. It is by no means intended to suggest that all these hours are equally preferred, and biting-peaks at some of them are very much more frequent than at others. For example, the writer's entire series of catches includes only two cases in which the highest level was attained in the period 01–02 hours, and both of these were rather poor. That quoted in Table VI, for example, is really a biphasic curve, and it may be noted in passing that biphasic curves are very common in this species. The argument is here confined to a single level, but it may be mentioned that the complexity of the picture is very materially increased when more than one level is studied.

Generally speaking, the mosquitos of this group are breeders in swamps, rivers and ground-pools. In many cases, they are much less selective for level than those of the first group. Thus, though in most series *T. africanus* is more abundant at ground level than in the canopy, there are localities where this distribution is reversed. Many of these points have been discussed by Lumsden (1952) who concludes that in this case the extensive nature of the breeding-grounds may lead to the development of very large populations, in which the necessity for longevity and for repeated ovipositions will be less than in the first group. He concludes on theoretical grounds that life is probably shorter in this second group and that therefore there will be a larger proportion of young females in the total population. He points out that in mosquitos of this type there is a minor wave of activity just after sunset, the main wave occurring later at night. He suggests that the small wave is made up of the older females, which are not very numerous, but which have accumulated during the day. A point, however, not made clear by Lumsden in his discussion is that the minor wave is not of regular occurrence. Working on the same platforms, the writer found that *A. gambiae*, for example, may not begin biting till two or three hours after sunset, or even much later. Lumsden's summed results show the small post-sunset wave as a matter of regular occurrence, varying only by minutes from season to season. This, however, does not take account of the fact that *A. gambiae* may begin biting in the canopy at any time of night. Thus in the Mongiro-Mamirimiri catches of 1944–45, the times at which *A. gambiae* began biting in the canopy were as follows:—

On 20 nights biting began in the period 18–19 hours.
,, 7 ,, ,, ,, ,, ,, ,, 19–20 ,,
,, 3 ,, ,, ,, ,, ,, ,, 20–21 ,,
,, 1 ,, ,, ,, ,, ,, ,, 21–22 ,,
,, 1 ,, ,, ,, ,, ,, ,, 22–23 ,,
,, 1 ,, ,, ,, ,, ,, ,, 23–24 ,,
,, 4 ,, ,, ,, ,, ,, ,, 00–01 ,,
,, 1 ,, ,, ,, ,, ,, ,, 03–04 ,,
,, 2 ,, ,, ,, ,, ,, ,, 04–05 ,,

Thus, on some nights *A. gambiae* did not begin biting in the canopy till just before sunrise. The results of the Bwamba Tree Survey were similar, *A. gambiae* being taken in the canopy on 77 nights in this series of 240 catches. The times at which it began biting at that level were as follows:—

On 21 nights biting began in the period 18–19 hours.
,, 8 ,, ,, ,, ,, ,, ,, 19–20 ,,
,, 9 ,, ,, ,, ,, ,, ,, 20–21 ,,
,, 7 ,, ,, ,, ,, ,, ,, 21–22 ,,
,, 6 ,, ,, ,, ,, ,, ,, 22–23 ,,
,, 26 ,, ,, ,, later than 23 hours.

Thus in the Mongiro-Mamirimiri series *A. gambiae* began biting in the canopy in the hour after sunset on only half the nights concerned. In the Bwamba Tree Survey the figure is even lower, being less than one-third of the nights on which this species occurred in the canopy.

It may be argued that in the writer's catches the ground-level unit may have tended to deflect specimens which in Lumsden's one-level catches would have come to bite in the canopy. This has not, however, proved to be the case with other species where a comparison of different methods is possible. In any event, however late biting begins in the canopy, it is usually initiated by a small wave similar to that described by Lumsden, and this seems to indicate that some particular section of the population does in fact initiate biting, though not always in the hour after sunset. Thus support is forthcoming for Lumsden's view, though not for that part of the hypothesis which is connected with the initiation of biting just after sunset. A point of some importance, however, whose full significance will be made more apparent below, is that while these minor waves are clear enough to affect the results for entire one-hour periods in the case of platform catches, they do not appear at ground-level, which is apparently the main habitat of *A. gambiae*.

The results shown in Table III for *Aëdes africanus* indicate that in the case of mosquitos of the first group the summation of results for successive nights may be a justifiable procedure. In the second group, however, the matter is much more difficult. For example, the summation of the figures shown in Table VI would not give information of real value, beyond indicating that *Taeniorhynchus africanus* is essentially nocturnal. Further, if the first four catches listed in Table VI be combined, they give an entirely different picture from the second or the third four, as is shown in fig. 3. It would be quite impossible to produce such divergent results in the case of a species such as *Aëdes africanus*.

In such a case as that of *Taeniorhynchus africanus*, it is tempting to abandon analysis at this stage, and to conclude that the biting-cycle, apart from a general nocturnal periodicity, is irregular. It has been found, however, that in the cases so far worked out in detail, it is possible to proceed much further with analysis and to obtain results which appear to be logical and of value in elucidating the behaviour of the mosquito concerned. After trying many methods, two in particular have proved useful.

In the first method summation is confined to the groups of days on which the biting-peak occurred within a particular hour or other selected period. This, of course, leads to an accentuation of the peak in the final figures, no matter whether the total or some form of average is used. The object of the method is not, however, primarily concerned with this effect. Its main purpose is to study the remainder of the curve, and to compare it with those for groups of days on which the peak occurred at a different time. Suppose, for example, that a given species showed a peak of biting-activity two hours after sunset on a certain group of days, and that the combined curve for these days showed also a minor but distinct peak two hours before sunrise; the main object of comparing this group of days with those on which the main peak occurred one, two or three hours later, would be to study this minor peak and to observe whether or not it was constantly present, and whether or not its magnitude and position in time remained relatively constant, or whether it moved similarly to the main peak, and so on.

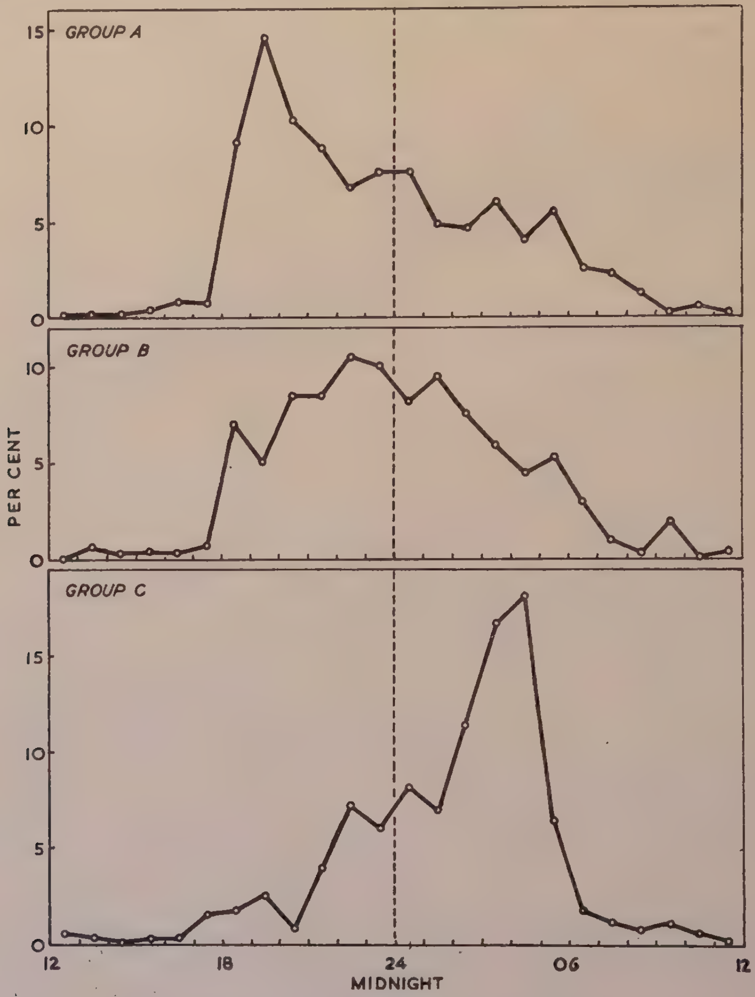


Fig. 3.—The biting-cycle of *Taeniorhynchus africanus* at ground-level, as shown by three groups of four catches each. Data selected from Table V. The figures are shown as percentages to facilitate comparison.

The second method is applicable mainly in cases where the biting-cycle occupies a part only of the 24 hours. In such cases examination of the detailed results will show that biting did not begin on all days at the same hour. In such cases, if the days are grouped by the time of initiation of the biting-cycle, a series of different but consistent biting-patterns will often emerge, which permit conclusions to be drawn. This method must be discussed in further detail, but it is convenient to do so at a later stage.

In this and subsequent sections certain criticisms of Lumsden's (1952) interpretation of the results of his sunset catches are made. At this point it should be made clear that the writer, while at present unable to agree with some of Lumsden's argument, feels that this author has produced suggestions of value and that, whether or not the detail of his views subsequently proves to be correct, the general outlook of the paper concerned is one which cannot be ignored in subsequent studies on mosquito-biting behaviour in nature.

The Use of Means and other Measures of the Central Tendency in Analysis.

In considering the combined results for a series of catches, it is usually necessary to employ some form of average for the various hour-groups. After trying many methods, the writer has concluded that the only satisfactory one involves the use of the geometric mean (M_G) as first discussed by Williams (1937, 1939).

In considering this point it seems best to use an actual example, and in this connection the biting-cycle of *Hodgesia cyptopus* is suitable. *H. cyptopus* is a tiny mosquito which bites viciously in forest and in plantations. It occurs at all levels, but is commonest at ground-level. It is almost exclusively diurnal, and bites most actively in the afternoon. The sample here discussed consists of 620 specimens taken in a series of five catches in a banana plantation at Zika, near Entebbe (Table VII).

Certain commonly-used measures of the central tendency such as the median and the mode are not of particular value in the present connection. While the median is useful in long series, it may be misleading in short ones such as the present. The mode is rarely a justifiable measure in the present type of work, as within each time-group the distribution of the results is frequently multimodal.

Certain other measures which have actually been used in previously published work on mosquitos may now be discussed. The first of these is the arithmetic mean. While useful in indicating a general trend, it is apt to be unduly influenced by extreme values, due to individual catches, and for this reason the writer is unable to regard its use as justified in the detailed analysis of catch results.

In the case of *H. cyptopus* the arithmetic mean shows a very smooth curve rising from sunrise to a well-defined peak at 15–16 hours, after which the numbers fall again rapidly (fig. 4). Of the various methods here discussed, the arithmetic mean is the only one which shows the peak activity as occurring in this period, and this effect is simply due to the occurrence of a single unusually large catch at this time. In all the other methods mentioned below, the peak occurs one hour earlier, in the period 14–15 hours.

As previously pointed out (Haddow & others, 1947*a*; Haddow & others, 1950), where disease transmission is involved, the regularity of occurrence of a biting insect at a given period day after day may be almost as important as its actual numbers. Thus a mosquito which is present in moderate numbers at a given period every day is likely to be a more effective vector than one which, though perhaps much more abundant, is irregular or intermittent in its appearance. The various methods now to be discussed all take this point into consideration in one way or another.

Mattingly (1949*a*) has attempted to overcome the effects of individual unusually large catches by reducing the figures for each day to percentages, by time groups. In the case of a series, he sums these percentages for each period, and then takes the mean. The results, in the present example, seem preferable to the arithmetic mean, in that the effect of the single large catch referred to above is reduced, and the biting-peak appears in the period 14–15 hours. Mattingly's method is, however, exceedingly laborious where long series are involved, and it is liable to at least one serious fallacy. Anyone who has had experience of mosquito work in the field will realise that catches vary enormously

TABLE VII.

The biting-cycle of *H. cyptopus* in a banana plantation at Entebbe.

Hour	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24
Total catch (620)	—	—	—	—	—	—	9	19	23	39	49	59	70	79	106	123	34	10	—	—	—	—	—	—
Days' occurrence	—	—	—	—	—	—	2	3	4	5	5	5	5	5	5	4	4	2	—	—	—	—	—	—
Arithmetic mean	—	—	—	—	—	—	1·8	3·8	4·6	7·8	9·8	11·8	14·0	15·8	21·2	24·6	6·8	2·0	—	—	—	—	—	—
The same, as percentage	—	—	—	—	—	—	1·5	3·1	3·7	6·3	7·9	9·5	11·3	12·7	17·1	19·8	5·5	1·6	—	—	—	—	—	—
Mean of daily percentages ..	—	—	—	—	—	—	1·5	2·9	3·7	5·2	8·4	9·2	11·1	14·9	19·5	17·1	5·5	1·0	—	—	—	—	—	—
Biting index	—	—	—	—	—	—	3·6	11·4	18·4	39·0	49·0	59·0	70·0	79·0	106·0	98·4	27·2	4·0	—	—	—	—	—	—
The same, as percentage	—	—	—	—	—	—	0·6	2·0	3·3	6·9	8·7	10·4	12·4	14·0	18·8	17·4	4·8	0·7	—	—	—	—	—	—
Geometric mean	—	—	—	—	—	—	0·78	2·13	2·73	5·19	8·38	10·53	10·22	14·63	15·75	12·00	4·97	1·82	—	—	—	—	—	—
The same, as percentage	—	—	—	—	—	—	0·9	2·4	3·1	5·8	9·4	11·8	11·5	16·4	17·7	13·5	5·6	2·0	—	—	—	—	—	—

Five 24-hour catches at ground-level. Results analysed by various measures of the central tendency.

TABLE VIII.

The biting-cycle of *Anopheles gambiae* at different levels, Mongiro, Bwamba, 1944–45.

Hour	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	Total
Arithmetic totals																									
54 feet	—	—	—	—	—	—	49	26	31	47	30	53	52	55	58	97	163	245	32	11	9	—	1	—	959
31 feet	—	—	1	—	—	—	91	59	52	96	89	95	92	88	148	213	440	440	64	12	1	2	—	—	1,983
16 feet	1	—	—	—	1	2	63	64	101	158	235	196	221	265	319	321	519	596	153	32	11	2	1	3	3,264
0 feet	15	46	36	63	114	129	393	544	589	754	851	865	844	1172	1251	1335	1251	1172	428	124	85	61	51	54	12,227
100 M_G																									
54 feet	—	—	—	—	—	—	155	86	77	121	110	198	202	230	251	388	646	1045	72	20	12	—	4	—	
31 feet	—	—	4	—	—	—	296	164	157	311	318	389	335	349	581	741	1961	1865	133	39	4	6	—	—	
16 feet	4	—	—	—	4	6	227	180	335	564	776	758	845	1103	1224	1206	2106	2500	380	83	20	7	4	9	
0 feet	51	105	87	100	198	335	1766	2426	2476	3514	3501	3817	3688	4993	5221	5905	5870	5011	1502	443	294	259	162	142	
M_G as percentage																									
54 feet	—	—	—	—	—	—	4·3	2·4	2·1	3·3	3·0	5·5	5·6	6·4	6·9	10·7	17·9	28·8	2·0	0·6	0·3	—	0·1	—	
31 feet	—	—	0·1	—	—	—	3·9	2·1	2·1	4·1	4·2	5·1	4·4	4·6	7·6	9·7	25·6	24·3	1·7	0·5	0·1	0·1	—	—	
16 feet	x	—	—	—	x	0·1	1·8	1·5	2·7	4·6	6·3	6·2	6·8	8·9	9·9	9·8	17·0	20·2	3·1	0·7	0·2	0·1	x	0·1	
0 feet	0·1	0·2	0·2	0·2	0·4	0·6	3·4	4·7	4·8	6·8	6·7	7·4	7·1	9·6	10·1	11·4	11·3	9·7	2·9	0·9	0·6	0·5	0·3	0·3	

in size from day to day. In the extreme case where only one mosquito of a given species is taken in 24 hours, it would represent 100 per cent. of the catch for that day, and this figure would have a profound effect on the results of even a long series of percentages for the hour concerned, involving much larger numbers of insects, but much lower percentages. Thus the fewer the number of hours in which a given species is taken on a given day, the greater will be the effect on the final results. In general, it is on unfavourable days when numbers are small that a biting-cycle will be abbreviated or rendered discontinuous by gaps of an hour or more, yet it is these days which will have the most profound effect on the figures for the periods concerned.

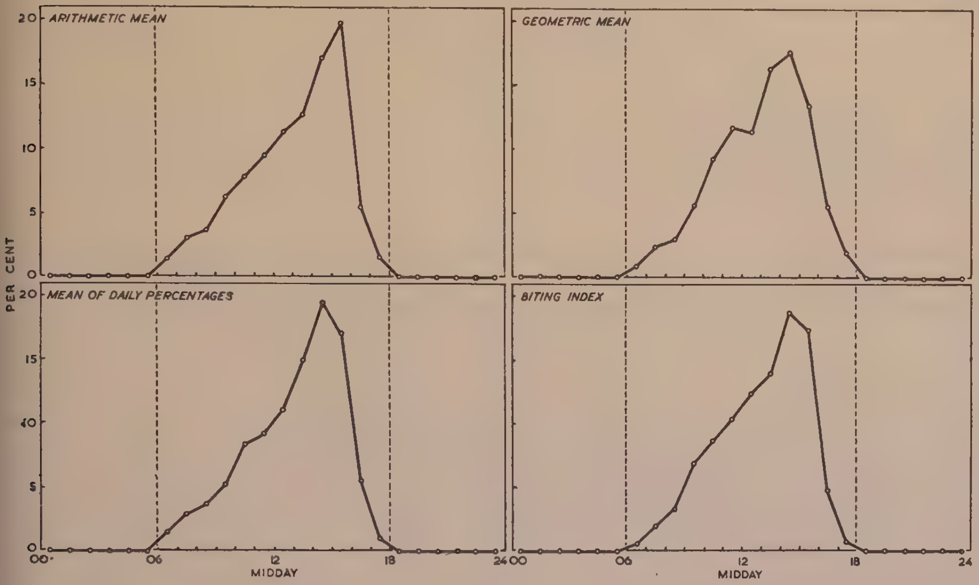


Fig. 4.—The biting-cycle of *Hodgesia cyptopus* in a banana plantation at Zika. Five 24-hour catches, to compare various methods of measuring the central tendency. The figures have been reduced to a percentage basis to facilitate comparison.

At a later date the writer attempted to work out a " biting index " which would take into account both regularity of occurrence and numbers taken. In its first form the index was computed by multiplying the arithmetic mean catch for a period by the number of days on which the species occurred at that period. Later it was concluded that as the arithmetic mean could not be regarded as a sound measure in mosquito work, the geometric mean should be used instead (Haddow & others, 1950). It was realised subsequently, however, that as the geometric mean itself tends to be influenced by the number of days' occurrence, the result was now unduly weighted in favour of days, as opposed to numbers, and it was concluded that the first method was preferable. It is used in the example here given (Table VII and fig. 4). An unsurmountable difficulty is, however, that while the index will reduce the value of a period where occurrence was irregular, it cannot enhance the value of one where occurrence was regular. Thus in the present instance *H. cyptopus* occurred in every day of the series in all the hours from 09 till 15. This whole section of the curve is therefore similar in trend to that given by the use of the arithmetic mean, and will repeat any errors introduced by the use of this measure. The index is useful in that it reduces the values in the periods of irregular occurrence near dawn and sunset, but even here it does not seem to have any advantage over the geometric mean, which will now be discussed.

The geometric mean of a series of figures is the *N*th root of their product (where *N* is their number). It is simply and rapidly computed by the use of logarithms even when long series are involved. An objection to its use was that it could not be employed in cases where zero values occurred in the series—an almost invariable occurrence in the case of field work on insects. Williams (1937) has, however, shown that this difficulty may be overcome by the use of log $(n + 1)$ instead of log n, one subsequently being subtracted from the final value. While the figure obtained is not the geometric mean *sensu stricto*, and should really be given a name of its own, this has not as yet been done, and for convenience the term " geometric mean " will be used here.

The use of this measure is based on the observation that " the changes that take place in the catches are of a geometric nature; that is to say, that a catch of double the mean is as likely to occur as one of half the mean; four times the mean is as likely to occur as one-quarter of the mean, etc." (Williams, 1939). Where a series is absolutely regular (in the present case, the same number of insects at the same hour, on every day concerned) the arithmetic and geometric means will be the same. In other cases the geometric mean will be smaller than the arithmetic.

In effect, the geometric mean reduces the influence of individual unusually large catches. In this way it takes some account of regularity of appearance, as zero values are much less likely to be counterbalanced by occasional very large catches than when crude figures are used. To give a concrete example, if in a series of five catches the results for two consecutive hours were as follows: Hour " a " —3, 2, 2, 1, 2—total 10; Hour " b "—6, 3, 0, 3, 0—total 12, then the arithmetic mean for hour " a " would be 2·0, and that for hour " b " 2·4. In the case of the geometric mean, however, hour " a " would show a higher figure (1·9) than hour " b " (1·6). Thus the effect of the unusually high catch of 6 in hour " b " on the first day fails to overcome the result of the two days on which no mosquitos were taken at this time. It remains to be said that examples of this kind, where the geometric mean may show quite a different picture from the arithmetic mean, are very common in actual practice. In very long series, of course, the effect is frequently less pronounced, particularly in the case of species which are regular in their behaviour. A good example is the biting-cycle of *A. africanus*. Here the results of a long series of catches showed the arithmetic and geometric figures following very much the same trend (Haddow & others, 1950).

Returning to the main example under discussion, the biting-cycle of *H. cyptopus*, it may be mentioned that the smoothness of the curve as shown by the methods discussed above is in itself quite obviously misleading. Even the most markedly diurnal mosquitos show, in the writer's experience, a tendency to bite less actively in the hottest part of the day, usually just after noon. This occurs even in such species as *Aëdes simpsoni* (Haddow, 1945*b*) and it has been noted in South America as well as in Africa (Kumm & Novis, 1938). The geometric means for *H. cyptopus* show a drop in activity in the period 12–13 hours, thus bringing its behaviour into line with that observed in other diurnal mosquitos, whereas all the other methods show the catch as increasing at this period, and give the fallacious impression of a species so conditioned for biting in heat and sunshine that its activity increases at a time when all others are experiencing a lull of greater or lesser degree. Once again, examination of the detailed results shows that the apparent rise in activity in the period 12–13 hours is due to an unusually large catch on a single day.

Thus in the example discussed, the results for two separate hour periods (12–13 and 15–16) tend to be influenced by single unusually large catches. The arithmetic mean gives an unsatisfactory picture of behaviour in both the periods concerned. By the use of mean percentages or the biting-index a correction is effected for one of them, but in the case of the geometric mean corrections are effected in both.

The author has, therefore, after a long trial of various methods, concluded that the geometric mean is the measure of choice where averages are to be used. Examples given so far in this paper have mostly been on an arithmetic basis, but from this point onward the geometric mean will be used except where stated otherwise. In most cases the writer has worked out this figure to two decimal places. It is useful, therefore, to multiply the results by 100, to give integer numbers, which save a considerable amount of space in tabulated results (should the geometric mean be worked out to three decimal places, then 1,000 is of course the appropriate multiplier). As a rule this figure, 100 or 1,000 M_G, has been found the most convenient for general use.

The Biting-Cycle at Different Levels.

When discussing the results of the first groups of stratified catches at Mongiro and Mamirimiri (Haddow & others, 1947*a*) the writers concluded that the results for all levels could be combined for study of the biting-cycle. Subsequent more detailed analysis has not, however, supported this view in every case.

In many instances it has been found that though the general trend at all levels may be the same, there are frequently differences of degree, which may be important. These tend to disappear when levels are combined, and the final curve usually approximates to that for the most favoured level, where the largest numbers are taken. A brief discussion of some of the original results for *Anopheles gambiae* will illustrate this point, a suitable example being the Mongiro sample of 1944–45.

This species always being much more abundant at ground-level than in the trees, the results for ground-level tend to swamp those for all the others when they are combined. When, however, the various levels are examined separately, the results shown in Table VIII and fig. 5 are obtained. Here it is seen that in the canopy (54 feet) and the understorey (31 feet) there is a distinct though minor peak in the hour after sunset. In the upper shrub layer (16 feet) it can still be detected, but at ground-level it is not apparent. Now, this peak, though small, may be important, as has been stressed by Lumsden (1952) and the fact that it is confined to levels above ground is of considerable interest.

Turning to the period of most active biting just before sunrise, other marked differences are found. Here the ground-level curve shows a massive wave of activity, prolonged over four to five hours. At 16 feet the wave is, relatively, much more pronounced, and it is also more clearly defined, being confined to two hours. The result at 31 feet is similar, but the relative magnitude of the wave has increased still further. Finally, in the canopy the wave forms a pronounced peak in the single hour before sunrise, this period yielding almost one-third of the total catch for the entire 24 hours.

A final point, which does not show well in the small-scale figure (more particularly as this is based on percentages), but which is at once apparent from the Table, is that a good deal of biting is able to continue at ground-level throughout the day, whereas at other levels there is very little, except in the early morning. This is shown most clearly by comparing the crude figures for the afternoon (*i.e.*, 12–18 hours) for the four levels, the results being as follows:—

Level	*Number taken*
54 feet	0
31 feet	1
16 feet	4
Ground-level	403

In the case of *A. gambiae*, however, the general trend may be said to be rather similar at all levels. Thus the results from any level will show clearly that this species is essentially nocturnal, reaching its main biting activity in the second half of the night. The differences, though important, are mainly of degree. In some species, however, the cycle at ground-level may be almost completely the reverse of that in the trees.

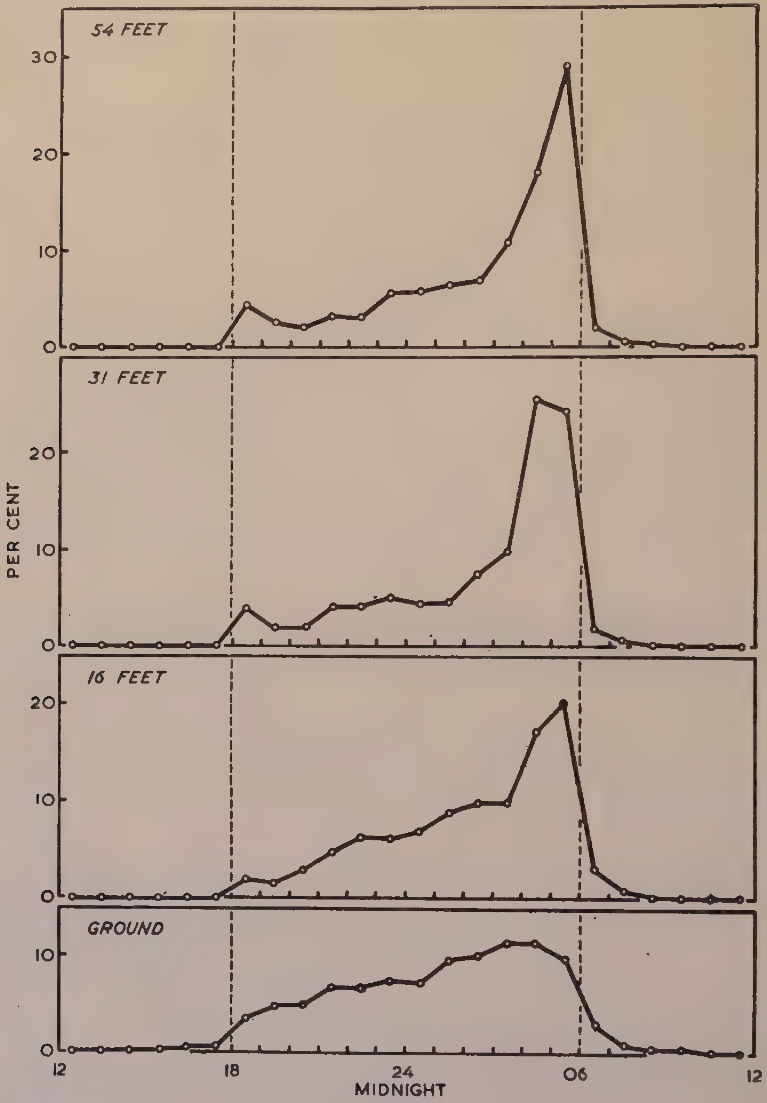


Fig. 5.—The biting-cycle of *Anopheles gambiae* at Mongiro, 1944–45, by hour and level, as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison.

To give an extreme example, the biting-cycle of *Taeniorhynchus pseudoconopas* may be mentioned. In the 35 catches at three levels carried out in forest near Entebbe the crude results were as follows:—

Level	*Caught by day*	*Caught by night*
Canopy	0	37
Understorey	1	36
Ground-level	24	3

Thus in the canopy, 100 per cent. of the catch was made by night, and in the understorey about 97 per cent. At ground-level, however, the reverse was the case, approximately 89 per cent. of the catch being taken by day. Such reversals are not uncommon, and they may occur in the case of important species, of which *Aëdes africanus* is a good example. The numbers of this species taken at ground-level always being very small, it was a long time before it was realised that by far the greater part of the ground-level catch was taken by day. This led eventually to interesting conclusions about vertical movements, which will be discussed further below.

The general conclusion is, therefore, that the results for different levels should rarely be combined, and then only after careful scrutiny.

Differences in Biting-Activity with Reference to Locality.

Whereas in the case of most species the biting-cycle in different localities, even on opposite sides of the continent, appears to show very constant characteristics, exceptions do occur, and these are sometimes of a puzzling nature.

A good example is to be found in the case of the biting-cycle of *Anopheles implexus* as observed at ground-level in the Entebbe area and in Bwamba. Here the results (Table IX and fig. 6) show that while near Entebbe *A. implexus* is largely diurnal, in Bwamba it is mainly nocturnal. The one curve is, actually, not far from being a mirror-image of the other.

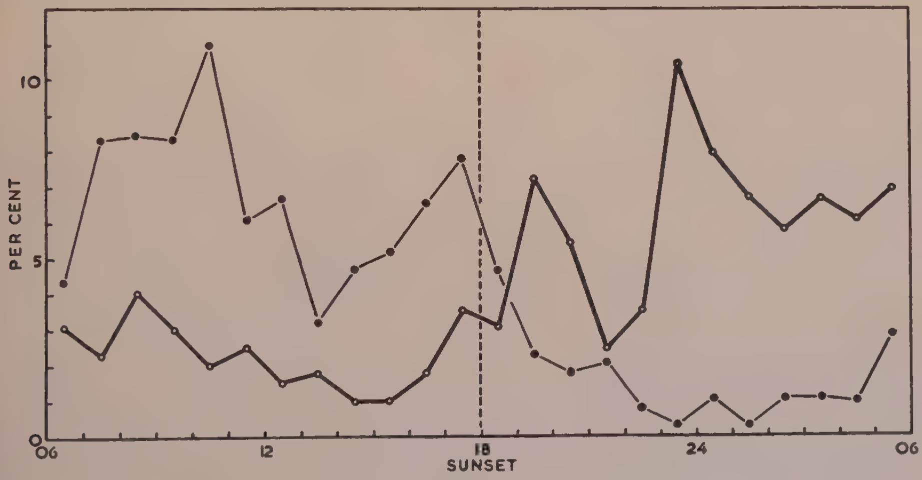


Fig. 6.—The biting-cycle of *Anopheles implexus* at ground-level in Bwamba and in the Entebbe area, as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison.

Another remarkable case occurs in *Aëdes africanus*. The biting-cycle of this species in the Lagos area (West Africa) closely resembles that at Entebbe and in Bwamba. In the Kenya coastal area, however, Lumsden (in press) has found that it is quite different, at least in one locality. In the Lumi river forest at Taveta he obtained 19 specimens in 24-hour catches, and of these 18 were taken by day. In all the other areas so far studied this species has been almost exclusively nocturnal.

TABLE IX.

The biting-cycle of *Anopheles implexus* at ground-level. A comparison of the figures obtained during the Bwamba and Entebbe Tree Surveys.

Hour	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	Totals
Entebbe totals	13	26	31	30	47	25	24	11	17	20	22	33	13	7	6	6	2	1	3	1	3	4	3	10	358
Geometric mean × 100	28	54	55	54	72	40	44	21	31	34	43	51	31	15	12	14	5	2	7	2	7	7	6	18	
Geometric mean as percentage	4·3	8·3	8·4	8·3	11·0	6·1	6·7	3·2	4·7	5·2	6·6	7·8	4·7	2·3	1·8	2·1	0·8	0·3	1·1	0·3	1·1	1·1	0·9	2·8	
Bwamba totals	7	5	8	6	4	5	3	4	2	2	4	7	6	14	14	5	7	18	16	13	15	21	17	15	218
Geometric mean × 100	19	14	25	18	12	15	9	11	6	6	11	22	19	44	33	15	22	63	48	41	35	41	37	42	
Geometric mean as percentage	3·1	2·3	4·1	3·0	2·0	2·5	1·5	1·8	1·0	1·0	1·8	3·6	3·1	7·2	5·4	2·5	3·6	10·4	7·9	6·7	5·8	6·7	6·1	6·9	

TABLE X.

The biting-cycle of *Anopheles gambiae* at canopy level (54 feet), Mongiro, Bwamba, in the wet season of 1944 (10 catches) and the dry season of 1945 (10 catches).

Hour	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	Total
Wet season, 1944																									
No. taken	—	—	—	—	—	—	38	24	28	41	22	33	33	30	29	45	92	164	22	9	9	—	—	—	619
100 M_G	—	—	—	—	—	—	306	200	163	244	179	242	247	225	262	359	730	1309	84	26	26	—	—	—	—
M_G as percentage ..	—	—	—	—	—	—	6·7	4·3	3·5	5·3	3·9	5·3	5·4	4·9	5·7	7·8	15·8	28·4	1·8	0·6	0·6	—	—	—	100·0
Dry season, 1945																									
No. taken	—	—	—	—	—	—	11	2	3	6	8	20	19	25	29	52	71	81	10	2	—	—	1	—	340
100 M_G	—	—	—	—	—	—	60	15	20	41	58	156	163	236	237	419	571	675	61	15	—	—	7	—	—
M_G as percentage ..	—	—	—	—	—	—	2·2	0·6	0·7	1·5	2·1	5·7	6·0	8·6	8·7	15·3	20·9	24·7	2·2	0·6	—	—	0·3	—	100·1

In the instances mentioned above the localities concerned are separated by long distances. Lumsden, however (in press), describes a case where the cycle of a mosquito differs in different environments in one locality. Working at Mida on the Kenya coast, he made catches of a salt-water breeder, *A. pembaensis*. In its breeding-ground, an *Avicennia* (black mangrove) orchard, the cycle showed biting throughout the night with a very marked peak in the hour after sunrise. In bush about 2 km. away, biting was almost completely confined to the second hour after sunset. Lumsden suggests that this occurs because in the bush, distant from the breeding-place, the population will contain a large percentage of old females which, released by the decline of light at sunset, are ready to bite at once, a theory discussed at greater length earlier in the present paper. He does not explain why in this case the peak should occur in the second rather than the first hour after sunset, and it seems likely that here he would have to postulate some factor other than light to explain the underlying mechanism.

The main point to be stressed in the present section is that in a given area, if the prevalence of a mosquito is to be gauged, it is not enough to catch during a peak period established by work somewhere else. It is first necessary to show that the biting-cycle is, in fact, similar in the two areas, after which a sample taken at the peak period can be regarded with greater confidence. The most extreme case is exemplified by *A. simpsoni*. Gillett (1951) has shown that in some parts of Uganda this mosquito bites man, while in others it does not. Thus, where *A. simpsoni* is concerned 24-hour catches are necessary, not merely to gauge incidence, but also to establish whether or not the local population bites man.

The Biting-Cycle with Reference to Season and the Estimation of Seasonal Incidence.

In most cases, seasonal differences do not seem to produce gross changes in the form of the biting-curve. At unfavourable times of year the cycle, in most cases, seems to follow its usual trend, though at a numerically lower level. Sometimes, however, changes do occur in some particular part of the cycle, and these may have a marked influence on the interpretation of the results.

The biting-cycle of *Anopheles gambiae* at Mongiro has already been discussed in another context, and here again it provides a useful example. The results for the canopy (54 feet) are shown in Table X and fig. 7, the series concerned being the 10 catches made in the wet season of 1944 and the 10 strictly comparable catches made in the dry season of 1945.

The main point of interest here centres on the earlier part of the night. In the dry season the general incidence during the first five hours of darkness is strikingly low, whether it be regarded on a numerical or on a percentage basis. When the reason for this is sought, the following facts emerge: In the ten wet season catches, biting began in the canopy in the period 18–19 hours on nine nights. On the tenth night it began in the following hour. In the dry season, the picture was entirely different, as follows:—

Biting began in the period 18–19 hours on 4 nights.
,, ,, ,, ,, ,, 19–20 ,, ,, 1 night.
,, ,, ,, ,, ,, 20–21 ,, ,, 1 ,,
,, ,, ,, ,, ,, 21–22 ,, ,, 1 ,,
,, ,, ,, ,, ,, 22–23 ,, ,, 1 ,,
,, ,, ,, ,, ,, 23–24 ,, ,, 1 ,,
,, ,, ,, ,, ,, 00–01 ,, ,, 1 ,,

Thus in the dry season biting in the canopy tended to begin irregularly, often very late, and with small numbers.

In the hour after sunset in the wet season, 6·7 per cent. of the geometric mean catch was taken, but in the dry season series the figure for this period was only 2·2 per cent. When, however, the figures for the last two hours of darkness are examined, it is found that in the wet season catches they form 44·2 per cent. of the total, and in the dry season 45·6 per cent.; a strikingly close correspondence.

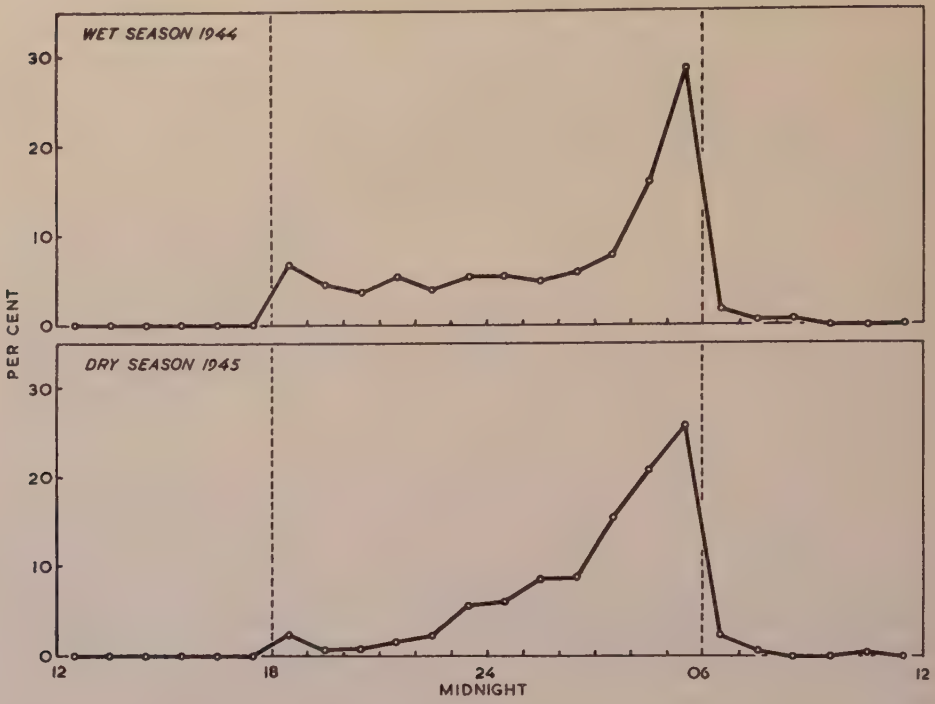


Fig. 7.—The biting-cycle of *Anopheles gambiae* in the forest canopy at Mongiro. Ten catches made in the wet season of 1944 compared with ten exactly similar catches made on the same platform in the dry season of 1945, as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison.

This example has been discussed at some length to show the sort of differences which may result from seasonal analyses. There remains the difficult subject of seasonal incidence in which, it is felt, the 24-hour catch may give results of considerable value.

Returning to Lumsden's evening catches at Mongiro, it is to be noted that he found a very marked seasonal fluctuation in the incidence of *A. gambiae*, catches yielding very high numbers in the rains and very low numbers in the dry weather. This seemed to be irreconcilable with the writer's experience of the same area which showed that at Mongiro and at the adjacent area of Mamirimiri there was only a slight diminution of the *A. gambiae* population in the dry weather, as shown by strictly comparable series of catches (Haddow & others, 1947*a*), the crude results for 24 periods being as follows:—

Locality	*Wet season 1944*	*Dry season 1945*	*Percentage reduction*
Mongiro	9898	8535	14
Mamirimiri	6294	5513	12

When however, the argument is confined to the period studied by Lumsden, *i.e.*, 15–21 hours, the result is very different, as follows:—

Locality	*Wet season 1944*	*Dry season 1945*	*Percentage reduction*
Mongiro	1542	829	46
Mamirimiri	950	496	48

It will be seen that the figures for the two areas are closely comparable, and it now seems likely that the apparent reduction noted by Lumsden is due simply to the fact that his estimate was based on a small part of the biting-cycle instead of on the whole 24-hour period. This becomes easily apparent when the curves shown in fig. 7 are compared, Lumsden's catches covering a period of activity which, always low, is strikingly reduced in the dry season.

The above discussion is based on the combined figures for all levels, which probably form the fairest comparison with Lumsden's work. Figures for 24-hour periods for the canopy alone may also be compared, but it is to be remembered that while his catches were made at one level only, the writer's were made at four. Thus insects which in the case of Lumsden's catches would have bitten in the canopy, may have been diverted to other levels in the writer's catches. The results are as follows:—

Locality	*Wet season 1944*	*Dry season 1945*	*Percentage reduction*
Mongiro	619	340	45
Mamirimiri	167	128	23

Here the reduction is much greater (being due to the tendency of *A. gambiae* to bite to a greater extent near ground-level in dry weather) but once more it is vastly exaggerated when the discussion is confined to the period 15–21 hours, the results being:—

Locality	*Wet season 1944*	*Dry season 1945*	*Percentage reduction*
Mongiro	90	16	82
Mamirimiri	21	7	67

In striking contrast to the above is the close agreement between Lumsden's results and the writer's for insects such as *Aëdes africanus* and *Chrysops centurionis*. The reason is, of course, that in this case Lumsden's catches covered the period of major incidence in the sunset period.

Thus it is evident that small seasonal changes in the form of a biting-cycle may affect quite profoundly the estimates for seasonal incidence, unless the whole 24-hour period is used.

Vertical Distribution.

While, broadly speaking, some mosquitos are essentially arboreal in their biting-habits and others prefer ground-level, it is important to remember that these preferences are only relative. Thus practically every species known to the writer may be taken from time to time in the forest canopy and similarly the species which frequent that level may also be taken in the understorey and at ground-level. Further, in the case of certain species reversals of the normal vertical distribution may take place. Thus *Taeniorhynchus africanus*, usually more prevalent at ground-level, will sometimes be found to be more abundant in the canopy at some particular station. In addition, it is to be remembered that seasonal alterations may occur (Haddow & others, 1947*a*).

An interesting point which emerged during the course of the Bwamba and Entebbe Tree Surveys, is that the vertical distribution of the arboreal species is related to the vegetation, and not to the actual height of the platforms. Thus the canopy stations in Bwamba ranged from 36 to 77 feet, but the mosquito fauna was very similar throughout. The same appears to be the case in the understorey as far as the present (more limited) experience goes. Generally speaking, the largest catches seem to occur at platforms which are well surrounded by foliage, regardless of the height of the canopy, and open or exposed stations are much less satisfactory.

Recently evidence has been obtained which indicates that at least some species have a cycle of vertical movement as well as a biting-cycle. In Bwamba, where the canopy is fairly dense and continuous, this is not a very well-marked phenomenon, and at first it was missed. In the lake shore forests near Entebbe, however, where the canopy is light, irregular, and often discontinuous, sun and wind penetrate to a much greater degree, and the phenomenon is well marked.

The matter was first noted when it was found that at Entebbe *Aëdes africanus* taken biting by day almost all came from ground-level. Later, it was noted that in the understorey the peak of biting-activity occurred in the hour before sunset, while in the canopy it did not occur till the hour after sunset. In theory, of course, this could be due to different populations with different biting-habits at the various levels, but direct observation in the understorey has shown that just at sunset *A. africanus* and many other mosquitos are, in fact, rising rapidly through the trees toward the canopy. This is most easily seen in the case of large pale species such as *T. fuscopennatus* and *T. aurites*, which are easily seen by lamplight. The dark *Stegomyia* spp. are much more difficult to observe. Just as the dusk and dawn periods are of great importance in relation to biting-cycles, so also are they important in relation to the whole question of vertical migrations.

The most clearly marked example of such movements so far found is that of *A. ingrami*. Here the figures from the Entebbe Tree Survey (Table XI and fig. 8) show that just after sunrise the canopy is the preferred level. By mid-morning, however, most of the biting population is at ground-level. After this the movement changes, and by mid-afternoon there are approximately as many in the understorey as at ground-level. In the two hours before sunset the understorey is the preferred level, but just after sunset a move to the canopy begins, and during the entire night the incidence in the canopy and understorey is approximately the same. In the Table and figure for this example the time-grouping is irregular, the groups having been selected to cover periods during which little change is taking place, but the hourly totals are also shown. At this stage there may be mentioned once more the case of *T. pseudoconopas* which at Entebbe bites almost exclusively at ground-level by day but in the trees at night.

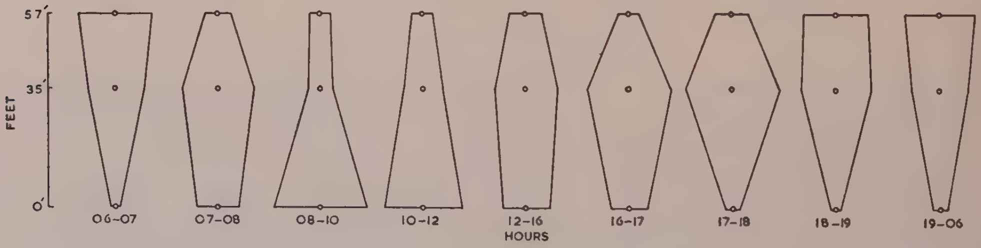


Fig. 8.—The vertical distribution of *Aëdes ingrami* at different periods of the day and night (Entebbe Tree Survey) as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison. The heights represent the mean for the seven stations.

TABLE XI.

The vertical distribution of *Aëdes ingrami* at different periods of the day and night, as shown by the Entebbe Tree Survey.

A. CRUDE HOURLY FIGURES Hour groups	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06
Arithmetic totals Canopy	13	5	4	1	1	4	5	1	0	3	7	37	22	8	5	2	1	3	2	4	2	3	2	5
Understorey	9	15	1	5	11	11	6	2	6	8	30	100	29	1	6	1	2	2	2	2	1	0	3	3
Ground-level	1	9	17	9	16	12	5	1	2	6	11	13	2	1	1	1	1	0	0	0	0	1	0	2

B. BY PERIODS Hour groups	06–07	07–08	08–10	10–12	12–16	16–17	17–18	18–19	19–06
Arithmetic totals Canopy	13	5	5	5	9	7	37	22	37
Understorey	9	15	6	22	22	30	100	29	23
Ground-level	1	9	26	28	14	11	13	2	7
100 M_G/hour Canopy	25	10	5	5	4	11	62	46	5
Understorey	19	29	6	10	8	47	177	51	4
Ground-level	2	17	22	19	6	20	26	4	1
M_G as percentage of total at the 3 levels Canopy	54	18	15	15	22	14	23	46	50
Understorey	41	52	18	29	44	60	67	50	40
Ground-level	4	30	67	56	33	26	10	4	10

Results such as these show that in the case of vertical distribution as in that of biting-activity, a study of the entire twenty-four-hour period is essential, if serious errors are to be avoided. Similarly it may be emphasised that in the case of vertical distribution the study of days' occurrence as opposed to simple numbers taken is just as important as in the instances discussed earlier in this paper. Once again, and for the same reasons, the geometric mean appears to be the most useful measure of the central tendency.

As has been mentioned above, the sunset and dawn periods are of particular importance in relation to vertical movements. It seems very likely that changes in light intensity may be the most important factor, as light is the only factor changing with sufficient rapidity at these times to explain some of the mosquito responses. Dr. J. C. Bugher has suggested, however, that very marked changes in the tension and layering of carbon dioxide may occur in forest at these times (private communication) and this is a point which certainly seems to call for further attention.

Obviously the whole subject of vertical movements is one of great importance where the transmission of a disease such as yellow fever is concerned. In this respect, however, it must again be emphasised that in the heavier rain-forests the movements appear—on present evidence—to be less well marked than in the light fringing forest of the Lake Victoria belt. Thus in the Semliki Forest *A. africanus* is never very common at ground-level, whereas in the Entebbe area it is quite common in the undergrowth by day.

Finally, it is necessary to emphasise that the behaviour of different sections of the population may be quite dissimilar, and that at present our information is confined to that part of the female population which is conditioned for biting at any given time. Thus at Entebbe, where, as has been mentioned above, biting females of *A. africanus* are quite common in the forest undergrowth by day, it is very difficult to find resting, blood-fed or pregnant females in the undergrowth at any time. They may well be in the canopy or the understorey, but at these levels a search for resting mosquitos is not feasible. The same applies to the males. Thus the writer has never seen a male *A. africanus* taken in nature even in the course of very extensive collections from the undergrowth of the Semliki Forest (where this species is abundant) and it seems not unlikely that this sex may spend most of its life in the canopy—or perhaps over it.

The Influence of Climate and Weather; the Question Whether Different Sections of the Population Bite at Different Times.

During the earlier stages of the investigation the writer inclined to the view that much of the biting-behaviour of mosquitos might be explained in terms of a response to a given set of microclimatic conditions (Haddow, 1945*a*; Haddow & others, 1947*a*). At a later stage, however, it began to appear that local weather might be still more important (Haddow & Mahaffy, 1949). Later still, other views have come to the fore.

Briefly, in the early stages of the investigation the writer felt that under a particular set of microclimatic conditions a given species would be conditioned for biting, and that the more closely these conditions were approached the more females would be taken biting. Even during the first set of 24-hour catches, however, it began to become apparent that under sets of microclimatic conditions apparently almost identical a given species might react in various different ways, and *vice versa*. During subsequent work the view that a mosquito is actively conditioned to bite by a suitable microclimate was gradually abandoned. In its place the view has developed that a mosquito may be restrained from biting by unfavourable microclimatic conditions or unfavourable local weather and that on removal of the unfavourable factors it may be " released " to bite.

Throughout the original investigations one of the greatest handicaps was that the mosquitos, required for inoculation into experimental animals in the attempt to isolate yellow fever virus, had to be identified while alive, and so could not be dissected. Current work by the writer has, however, shown that Culicines of various species bite (in nature) at a particular phase in the ovarian cycle, namely, late in Egg Stage I or early in Egg Stage II (using the egg stages of Christophers, as described by Christophers, Sinton and Covell, 1936). This applies not only to the first ovarian cycle, but to subsequent cycles as well, as has been shown unequivocally by cases where fully mature eggs left over from a previous oviposition have been found in an ovary otherwise early in Stage II. Thus it may be that feeding activity bears a relatively constant relationship to ovarian development, though microclimate and weather may have an important restraining influence during certain parts of the 24-hour cycle. In captivity, of course, repeated blood meals may be taken during a single ovarian cycle, and in captive *A. africanus* and *A. ruwenzori* the writer has found that some mosquitos may feed every second day or even daily. In this connection, however, it should be emphasised that the ovarian cycle in captivity and in nature may be very different things. Thus Muirhead Thomson (1951*a*) places the gonotrophic cycle of *Anopheles gambiae* at 2–3 days, whereas in captive specimens in Uganda the writer has seen it prolonged to as much as a week or ten days. Present indications are that in nature biting does take place at a relatively well-fixed point in the cycle, at least for those Culicines so far studied.

Certain factors, notably wind, seem always to be antagonistic to biting. This was noted in mosquitos entering huts at Kisumu by the writer (1942) and by Haddow and Mahaffy (1949) in forest mosquitos. More recently the effects of wind in the crepuscular period have been discussed in greater detail by Lumsden (1952).

With reference to possible release mechanisms, the most important microclimatic factor must almost certainly be light. Thus a large number of species cease biting at sunset, while others begin to bite at this time, and much the same is true of sunrise. The speed with which many of these changes of behaviour occur is such that it can be attributed only to the rapid light changes of these periods in the tropics. No other factor changes with sufficient suddenness to explain the facts. This was emphasised by Haddow and Mahaffy (1949) in the case of *Aëdes africanus*, by Haddow & others (1950) in the case of *Chrysops centurionis* and *A. africanus*, and recently Lumsden (1952) has contributed a detailed discussion on the subject as it affects various species active in the crepuscular period.

Apart from release phenomena in the dawn and sunset periods, almost certainly due to rapid changes in light intensity, the behaviour of many species completely fails to respond to analysis in terms of any of the ordinary microclimatic factors. Here *A. nigerrimus*, an arboreal mosquito, provides a suitable example. In this species it may be presumed that light has an inhibiting influence, as the mosquito is almost exclusively nocturnal in its biting-habits. Biting begins just after sunset and increases steadily till a little before midnight, after which it declines steadily until sunrise (Table XII and fig. 9). It is obvious that such a cycle cannot be correlated with microclimatic changes during the hours of darkness. Thus temperature falls slowly from sunset till dawn, relative humidity remains very high and saturation deficiency very low (Haddow, 1945*a*) in the type of forest in which this species is to be found. On the other hand, while such a biting-cycle as this cannot readily be explained in terms of direct environmental influence, it may easily be explained in various other ways, of which the following is one example. Working on *Anopheles minimus* Theo. in Assam, Muirhead Thomson (1940) found that oviposition normally takes place at night; that about 69 per cent. of eggs are laid in the first third of the night, 22 per cent. in the second, and only 9 per cent. in the last third. If it were postulated that the

TABLE XII.

The biting-cycle of *Aëdes nigerrimus* in the canopy, as shown by the Bwamba Tree Survey.

Hour	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	Total
Arithmetic totals	—	—	—	2	—	—	8	11	14	18	26	26	22	15	11	15	7	2	1	—	—	—	—	—	178
1000 M_G	—	—	—	9	—	—	38	46	67	74	114	104	82	64	52	61	30	9	5	—	—	—	—	—	—
M_G as percentage ..	—	—	—	1·2	—	—	5·0	6·1	8·9	9·8	15·1	13·8	10·8	8·5	6·9	8·1	4·0	1·2	0·7	—	—	—	—	—	100·1

TABLE XIII.

The biting-cycle of *Aëdes longipalpis* in the canopy, as shown by the Bwamba Tree Survey.

Hour	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	Total
Arithmetic totals	—	—	—	—	—	—	2	9	22	50	77	101	115	129	145	122	59	17	5	3	—	3	—	—	859
1000 M_G	—	—	—	—	—	—	6	25	63	140	223	293	327	352	384	311	140	47	14	8	—	8	—	—	—
M_G as percentage ..	—	—	—	—	—	—	0·3	1·1	2·7	6·0	9·5	12·5	14·0	15·0	16·4	13·3	6·0	2·0	0·6	0·3	—	0·3	—	—	100·0

oviposition habits of *Aëdes nigerrimus* were similar, and further that biting followed oviposition, then the biting-cycle would at once become explicable.

To carry the argument further, it may be stated that in any case curves of such apparent simplicity have become rather suspect. A good example is shown by *A. longipalpis*, as represented in the arboreal section of the Bwamba Tree Survey. The general curve, as shown in Table XIII and fig. 10 is one of extreme simplicity, with a single well-marked peak in the period 14–15 hours. When, however, the starting-point of activity is studied, it is found that biting may begin at any hour between sunrise and sunset. If now all the days on

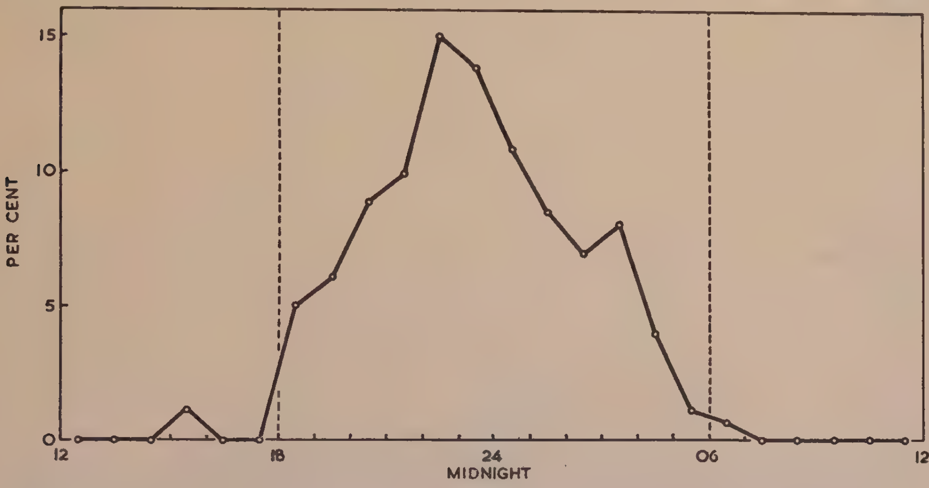


Fig. 9.—The biting-cycle of *Aëdes nigerrimus* in the forest canopy (Bwamba Tree Survey) as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison with other graphs.

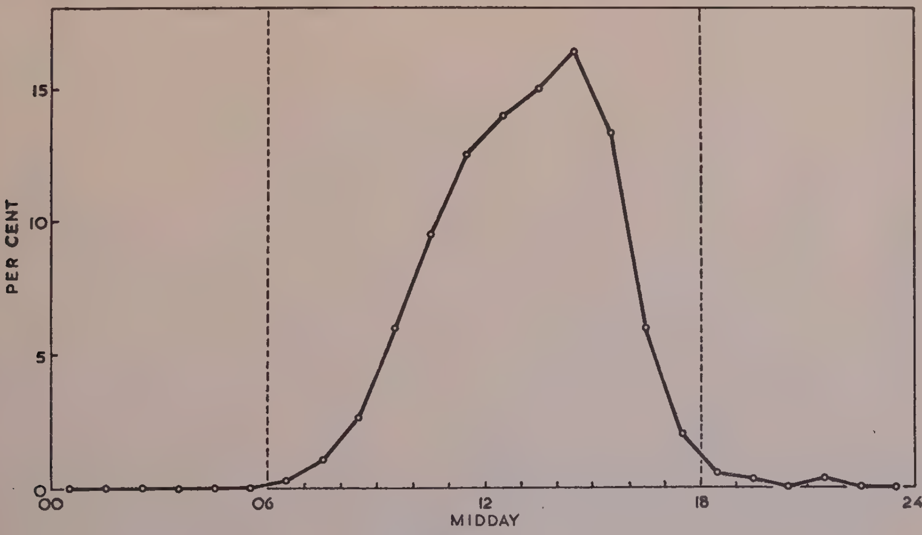


Fig. 10.—The biting-cycle of *Aëdes longipalpis* in the forest canopy (Bwamba Tree Survey) as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison with other graphs.

which biting began at some particular hour are considered as a separate group, a very different picture results. For the present purpose the 28 days on which biting began in the period 09–10 hours, the 37 days on which it began in the period 10–11 hours, and the 28 days on which it began in the period 11–12 hours form a suitable example (Table XIV and fig. 11). It at once becomes apparent that on each of these groups of days the curve is biphasic, with a major peak in the morning and a minor peak in the afternoon, and consequently that the apparently simple biting-curve of *A. longipalpis* is actually the resultant of a number of complex curves. Without wishing to discuss the whole sample in detail at this stage, the writer suggests that the curves in the present example imply that two separate groups in the population bite at different times. Thus the later the biting begins in the morning, the higher relatively does the morning peak become. On the other hand the percentage of the total catch taken before midday changes relatively little. On days when biting began in the period 09–10 hours, 38·2 per cent. of the total were taken before midday; on days when biting began in the period 10–11 hours the figure was 39·7 per cent., and on days when biting began in the period 11–12 hours it was 52·1 per cent. Thus, if a restraining factor be postulated, then the later it is removed, the greater proportionately is the wave of activity which follows. On the other hand, the minor wave of the afternoon remains almost unaffected by the proportions and time disposition of the morning wave; on the three groups of days the small afternoon peak in the period 14–15 hours was 14·5, 14·2 and 13·9 per cent., respectively. This remarkable constancy seems to indicate clearly a section of the population entirely unaffected by the morning behaviour. Information as to what these separate groups may be is not as yet available, and there are very many phases in the life of the female mosquito which might apply. There are, for example, the pre- and post-copulation groups, there is the first as opposed to all other ovarian cycles, and so on. In many ways it seems, as mentioned above, that the behaviour of this species supports the views advanced by Lumsden (1952) though

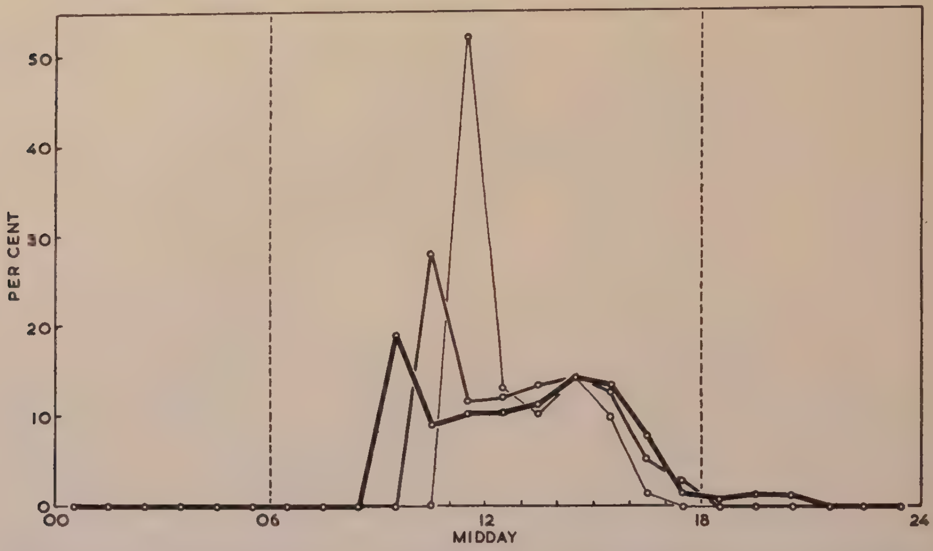


Fig. 11.—The biting-cycle of *Aëdes longipalpis* in the forest canopy (Bwamba Tree Survey) as shown by geometric means. These have been reduced to a percentage basis to facilitate comparison. Groups of days on which biting first began in the periods 09–10 hours (thick line), 10–11 hours (medium line) and 11–12 hours (thin line).

TABLE XIV.

The biting-cycle of *Aëdes longipalpis* in the canopy, as shown by the Bwamba Tree Survey, for groups of days on which biting began at different clock hours.

	Hour	00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	Total
A	Arithmetic totals ..	—	—	—	—	—	—	—	—	—	33	19	22	24	33	39	41	22	3	2	3	3	—	—	—	244
	100 M_G	—	—	—	—	—	—	—	—	—	114	54	61	62	68	87	80	47	8	5	7	7	—	—	—	—
	M_G as percentage ..	—	—	—	—	—	—	—	—	—	19·0	9·0	10·2	10·3	11·3	14·5	13·3	7·8	1·3	0·8	1·2	1·2	—	—	—	99·9
B	Arithmetic totals ..	—	—	—	—	—	—	—	—	—	—	48	26	26	31	32	29	12	7	—	—	—	—	—	—	211
	100 M_G	—	—	—	—	—	—	—	—	—	—	122	51	53	59	62	55	22	12	—	—	—	—	—	—	—
	M_G as percentage ..	—	—	—	—	—	—	—	—	—	—	28·0	11·7	12·2	13·5	14·2	12·6	5·1	2·8	—	—	—	—	—	—	100·1
C	Arithmetic totals ..	—	—	—	—	—	—	—	—	—	—	—	36	12	10	14	9	1	—	—	—	—	—	—	—	82
	100 M_G	—	—	—	—	—	—	—	—	—	—	—	124	31	24	33	23	3	—	—	—	—	—	—	—	—
	M_G as percentage ..	—	—	—	—	—	—	—	—	—	—	—	52·1	13·0	10·1	13·9	9·7	1·3	—	—	—	—	—	—	—	100·1

A, 28 days on which biting began between 09 and 10 hours; B, 37 days on which biting began between 10 and 11 hours; C, 28 days on which biting began between 11 and 12 hours.

here the release mechanism must be even more complex than the simple light release at sunset. Further, there is at the moment no particular reason to suppose that the two groups necessarily represent the old and young sections of the population.

The most important implication of this point of view—that different sections of the population may possibly bite at different times—is connected with disease transmission, as here only those mosquitos which are feeding for a second or subsequent time can pass on viruses or parasites to a susceptible host. Thus the actual transmission of a disease might well be confined to some very short period (as has been pointed out by Lumsden, 1952) and the most logical way in which to detect infection in the mosquito population or to gauge its incidence would be to study the females coming to bite at the time concerned. It is felt that further work on these lines might pay considerable dividends, particularly in the case of malaria, always provided that the old females could be recognised without doubt. In *Anopheles* the method described by Mer (1932) appears to provide a useful approach to the problem but in Culicines the matter may be much more difficult, as in various species the writer has examined he has failed to detect the dilatations in the oviduct which Mer has described for *Anopheles*.

The Impulse to Bite, and Related Subjects.

A good deal of work on the impulse to bite and on the attraction of the mosquito to the host has been done in the laboratory, particularly in the case of *Aëdes aegypti*. Such papers as those of Seaton and Lumsden (1941), Lumsden (1947) and Parker (1948, 1952), to mention only a few, have served to indicate the complexity of this difficult subject. A discussion of work of this type lies beyond the scope of the present communication, but some notes may be given on certain aspects of the subject which can be studied in the field.

Firstly, the stimulus in the case of a few diurnal species seems to be visual. This seems to be true of the genus *Eretmapodites* in general, and observations can easily be made on *E. chrysogaster*, which is sometimes exceedingly common and which, being large and light in colour, is easy to watch in nature. If a human bait takes up a position in forest at a time when this species is active (a suitable time is about an hour before sunset) he will probably be attacked almost at once. Most, if not all, the mosquitos will bite him below the knee. Some will engorge and others will merely fly round the bait or probe. Within a very short time all will have returned to their resting places on the leaves or low undergrowth. If the bait now stands perfectly still he will be approached by very small numbers only. As soon as he moves his legs, however, many females will take off and fly in directly. The straight, fast, purposeful flight of *E. chrysogaster* on such occasions is very interesting to watch, and is quite different from the vague and indirect approach of most other species, for which olfactory stimuli probably play a major part, particularly at night.

Coupled with this direct approach of *E. chrysogaster* (which may also be seen in other members of the genus and in *A. simpsoni*) its curious habit of taking interrupted blood-meals should be noted. Though in captivity and occasionally in nature it may alight and engorge at once, more commonly it will break off and return to the undergrowth. After a few minutes it will return for a further feed, and this process may even be repeated a third time.

As has been indicated above, movement seems to play a part in attracting *E. chrysogaster* to a standing bait. It must be emphasised, however, that this holds good only within a certain very restricted vertical zone. In a field experiment, 335 *E. chrysogaster* bit a standing bait over a period of 3½ hours. Of these, none bit above the hip line (great trochanter). Eight (3 per cent.) bit between the hip line and the knee, and 327 (97 per cent.) below the knee. Of the 327 almost all were taken between the ankle and the knee, and hardly any on the foot. It thus became apparent that in this species biting is confined to a very narrow band, roughly one foot deep, and extending from about 6 inches to 18 inches above the forest floor. This view was confirmed by making the bait lie down. If he lay flat on his back several *Eretmapodites* (when he made movement) would fly in at once and circle freely just over him, but very few would bite. If he lay on one side, to raise the " target " a little, many would bite at once, and the same result followed when he lay on a small tree-trunk, which raised him about six inches.

The above is an example of a mosquito which rests on the vegetation until an apparent source of food arrives, after which it takes off to investigate. In other ways also it is very specialised, being a small-container breeder confined to dense vegetation such as forest and plantations, the larva is a facultative predator (Haddow, 1946) and, as mentioned above, there is a marked preference for biting at a particular time, and within a very restricted level. It seems likely, however, that most species, particularly the less specialised mosquitos, do not remain resting until a source of food is apparent. Thus huge swarms of *Taeniorhynchus* spp. may be found far from their breeding-places, and this is also true of species like *Anopheles gambiae*. It is felt that these mosquitos seek for food actively, on the wing. How many of them ever do find a blood-meal is quite another question, and one to which at the moment no answer can be given. In the vicinity of a tropical swamp the numbers are often so overwhelming that it seems inconceivable that more than quite a small proportion can ever obtain a blood-meal.

Finally the curious fact should be mentioned that many species seem to arrive to bite in successive waves, at short intervals. This is particularly noticeable in the case of *Aëdes simpsoni*, where waves of biting activity occur at intervals of approximately fifteen minutes. This short-term periodicity cannot at the moment be explained either in terms of microclimatic influence, or in terms relating to different sections of the population. Another species which shows a similar periodicity on occasion is *T. africanus*, and on one night the writer had an opportunity of watching the phenomenon rather closely. The distribution of bites on a standing bait was being recorded in an area where this species is particularly abundant—the lake shore at Nakiwogo, Entebbe. The first point noted was that the mosquitos arrived to bite in waves at about 5-minute intervals. The second was that they all arrived downwind (there was a very gentle breeze) and the third that, having engorged, they continued downwind after taking off. This short-duration wave phenomenon is obviously one of considerable interest, but at the moment it is not possible to do more than to note its existence.

Summary and Conclusions.

It is felt that the 24-hour catch presents a valuable method of studying the biting-behaviour of mosquitos in the field, and further that conclusions concerning seasonal abundance, vertical distribution and times of biting-activity must be based on catches of this type if serious errors of interpretation are to be avoided.

The time-divisions of the catch should not exceed one hour, and even shorter intervals may be desirable. Timing should be related to the actual times of sunrise and sunset. Where possible, a series of consecutive catches should be carried out, and a shift system must be carefully considered in relation to the particular series projected.

Usually the results from different levels above ground should be treated separately in working out biting-cycles, and this may also apply to results from different seasons or different localities. Further, while in some instances the summation of long series of catches seems permissible, in others it is not, and in these detailed analysis of the figures may be necessary before consistent behaviour-patterns become apparent.

In cases where a measure of the central tendency is to be employed, the geometric mean as modified by C. B. Williams appears to be the most suitable.

It is no longer felt that the biting-behaviour of mosquitos in the field is actively conditioned by the influence of microclimate. Instead, it is suggested that the biting impulse is inhibited by unfavourable microclimatic conditions. When these become favourable the mosquitos are "released" to bite. Thereafter present evidence suggests that the biting-pattern which evolves is related more to separate groups in the female population than to the influence of the environment. It is now known that various species bite at a very constant phase early in the ovarian cycle.

Quite apart from this it appears that the biting-impulse is not the same in all species, some at least appearing to respond to visual stimuli. In addition, some mosquitos, quite apart from their main biting-pattern, come in small waves of short duration and at short intervals, a phenomenon which cannot at the moment be explained.

References.

Bates, M. (1944*a*). Observations on the distribution of diurnal mosquitoes in a tropical forest.—Ecology, **25,** pp. 159–170.

Bates, M. (1944*b*). Notes on the construction and use of stable traps for mosquito studies.—J. nat. Malar. Soc., **3,** pp. 135–145.

Bauer, J. H. (1928). The transmission of yellow fever by mosquitoes other than *Aëdes aegypti*.—Amer. J. trop. Med., **8,** pp. 261–282.

Bugher, J. C., Boshell-Manrique, J., Roca-Garcia, M. & Osorno-Mesa, E. (1944). Epidemiology of jungle yellow fever in eastern Colombia.—Amer. J. Hyg., **39,** pp. 16–51.

Christophers, S. R., Sinton, J. A. & Covell, G. (1936). How to do a malaria survey.—Govt. of India Health Bull. No. 14 (Delhi). 3rd edn., 206 pp.

Davis, D. E. (1944). A comparison of mosquitoes captured with an avian bait at different vegetational levels.—Rev. Ent., Rio de J., **15,** pp. 209–215.

Evans, A. M. (1938). Mosquitoes of the Ethiopian Region. II. Anophelini, adults and early stages.—404 pp., London, Brit. Mus. (Nat. Hist.).

Gillett, J. D. (1951). The habits of the mosquito *Aëdes (Stegomyia) simpsoni* Theobald in relation to the epidemiology of yellow fever in Uganda.—Ann. trop. Med. Parasit., **45,** pp. 110–121.

Haddow, A. J. (1942). The mosquito fauna and climate of native huts at Kisumu, Kenya.—Bull. ent. Res., **33,** pp. 91–142.

Haddow, A. J. (1945*a*). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—Bull. ent. Res., **36,** pp. 33–73.

Haddow, A. J. (1945*b*). The mosquitoes of Bwamba County, Uganda. III. The vertical distribution of mosquitoes in a banana plantation and the biting cycle of *Aëdes (Stegomyia) simpsoni* Theo.—Bull. ent. Res., **36,** pp. 297–304.

Haddow, A. J. (1946). The mosquitoes of Bwamba County, Uganda. IV. Studies on the genus *Eretmapodites*, Theobald.—Bull. ent. Res., **37,** pp. 57–82.

Haddow, A. J. (1952). Further observations on the biting-habits of Tabanidae in Uganda.—Bull. ent. Res., **42,** pp. 659–674.

Haddow, A. J. & Dick, G. W. A. (1948). Catches of biting Diptera in Uganda with anaesthetised monkeys as bait.—Ann. trop. Med. Parasit., **42**, pp. 271–277.

Haddow, A. J., Dick, G. W. A., Lumsden, W. H. R. & Smithburn, K. C. (1951). Monkeys in relation to the epidemiology of yellow fever in Uganda.—Trans. R. Soc. trop. Med. Hyg., **45**, pp. 189–224.

Haddow, A. J., Gillett, J. D. & Highton, R. B. (1947*a*). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate. —Bull. ent. Res., **37**, pp. 301–330.

Haddow, A. J., Gillett, J. D., Mahaffy, A. F. & Highton, R. B. (1950). Observations on the biting-habits of some Tabanidae in Uganda, with special reference to arboreal and nocturnal activity.—Bull. ent. Res., **41**, pp. 209–221

Haddow, A. J. & Mahaffy, A.F. (1949). The mosquitoes of Bwamba County, Uganda. VII. Intensive catching on tree-platforms, with further observations on *Aëdes* (*Stegomyia*) *africanus*, Theobald.—Bull. ent. Res., **40**, pp. 169–178.

Haddow, A. J., Smithburn, K. C., Dick, G. W. A., Kitchen, S. F. & Lumsden, W. H. R. (1948). Implication of the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald in the forest cycle of yellow fever in Uganda.—Ann. trop. Med. Parasit., **42**, pp. 218–223.

Haddow, A. J., Smithburn, K. C., Mahaffy, A. F. & Bugher, J. C. (1947*b*). Monkeys in relation to yellow fever in Bwamba County, Uganda.—Trans. R. Soc. trop. Med. Hyg., **40**, pp. 677–700.

Johnson, C. G. (1950*a*). A suction trap for small airborne insects which automatically segregates the catch into successive hourly samples.—Ann. appl. Biol., **37**, pp. 80–91.

Johnson, C. G. (1950*b*). The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small airborne insects.—Ann. appl. Biol., **37**, pp. 268–285.

Johnson, C. G. (1951). The study of wind-borne insect populations in relation to terrestrial ecology, flight periodicity, and the estimation of aerial populations.—Sci. Progr., no. 153, pp. 41–62.

Kerr, J. A. (1933). Studies on the abundance, distribution and feeding habits of some West African mosquitos.—Bull. ent. Res., **24**, pp. 493–510.

Kumm, H. W. & Novis, O. (1938). Mosquito studies on the Ilha de Marajó, Pará, Brazil.—Amer. J. Hyg., **27**, pp. 498–515.

Lumsden, W. H. R. (1947). Observations on the effect of microclimate on biting *Aëdes aegypti* (L.) (Dipt. Culicid.).—J. exp. Biol., **24**, pp. 361–373.

Lumsden, W. H. R. (1951). Probable insect vectors of yellow fever virus, from monkey to man, in Bwamba County, Uganda.—Bull. ent. Res., **42**, pp. 317–330. uo 2

Lumsden, W. H. R. (1952). The crepuscular biting-activity of insects in the forest canopy in Bwamba, Uganda; a study in relation to the sylvan epidemiology of yellow fever.—Bull. ent. Res., **42**, pp. 721–760. uo 78

LUMSDEN, W. H. R. & BUXTON, A. P. (1951). A study of the epidemiology of yellow fever in West Nile District, Uganda.—Trans. R. Soc. trop. Med. Hyg., **45**, pp. 53–78.

MAGOON, E. H. (1935). A portable stable trap for capturing mosquitos.—Bull. ent. Res., **26**, pp. 363–369.

MAHAFFY, A. F., SMITHBURN, K. C., JACOBS, H. R. & GILLETT, J. D. (1942). Yellow fever in western Uganda.—Trans. R. Soc. trop. Med. Hyg., **36**, pp. 9–20.

MATTINGLY, P. F. (1949*a*). Studies on West African forest mosquitos. Part I. The seasonal distribution, biting cycle and vertical distribution of four of the principal species.—Bull. ent. Res., **40**, pp. 149–168.

MATTINGLY, P. F. (1949*b*). Studies on West African forest mosquitos. Part II. The less commonly occurring species.—Bull. ent. Res., **40**, pp. 387–402.

MER, G. (1932). The determination of the age of *Anopheles* by differences in the size of the common oviduct.—Bull. ent. Res., **23**, pp. 563–566.

MUIRHEAD THOMSON, R. C. (1940). Studies on the behaviour of *Anopheles minimus*. Part I. The selection of the breeding place and the influence of light and shade.—J. Malar. Inst. India, **3**, pp. 265–294.

MUIRHEAD THOMSON, R. C. (1948). Studies on *Anopheles gambiae* and *A. melas* in and around Lagos.—Bull. ent. Res., **38**, pp. 527–558.

MUIRHEAD THOMSON, R. C. (1951*a*). Studies on salt-water and fresh-water *Anopheles gambiae* on the East African coast.—Bull. ent. Res., **41**, pp. 487–502.

MUIRHEAD THOMSON, R. C. (1951*b*). Mosquito behaviour in relation to malaria transmission and control in the tropics.—219 pp., London, Arnold.

PARKER, A. H. (1948). Stimuli involved in the attraction of *Aëdes aegypti*, L., to man.—Bull. ent. Res., **39**, pp. 387–397.

PARKER, A. H. (1952). The effect of a difference in temperature and humidity on certain reactions of female *Aëdes aegypti* (L.).—Bull. ent. Res., **43**, pp. 221–229.

SEATON, D. R. & LUMSDEN, W. H. R. (1941). Observations on the effects of age, fertilisation and light on biting by *Aëdes aegypti* (L.) in a controlled microclimate.—Ann. trop. Med. Parasit., **35**, pp. 23–36.

SHANNON, R. C. (1939). Methods for collecting and feeding mosquitoes in jungle yellow fever studies.—Amer. J. trop. Med., **19**, pp. 131–138.

SMITHBURN, K. C. & HADDOW, A. J. (1946). Isolation of yellow fever virus from African mosquitoes.—Amer. J. trop. Med., **26**, pp. 261–271.

SMITHBURN, K. C., HADDOW, A. J. & LUMSDEN, W. H. R. (1949). An outbreak of sylvan yellow fever in Uganda with *Aëdes (Stegomyia) africanus* Theobald as principal vector and insect host of the virus.—Ann. trop. Med. Parasit., **43**, pp. 74–89.

WILLIAMS, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—Ann. appl. Biol., **24**, pp. 404–414.

WILLIAMS, C. B. (1939). An analysis of four years' captures of insects in a light trap. Part I. General survey; sex proportion; phenology; and time of flight.—Trans. R. ent. Soc. Lond., **89**, pp. 79–131.

PULLUS IMPEXUS (MULS.) (COLEOPTERA, COCCINELLIDAE), A PREDATOR OF *ADELGES PICEAE* (RATZ.) (HEMIPTERA, ADELGIDAE), WITH NOTES ON ITS PARASITES.*

By Vittorio Delucchi.

European Laboratory of the
Commonwealth Institute of Biological Control,
Feldmeilen (Zurich).

9

E.M.

(Plates XI–XXVIII.)

Contents.

PAGE

Introduction 244

Method of rearing and techniques employed in the study of *Pullus impexus* 246
    Rearing in the laboratory 246
    Fixation of the material 247
    Microscopic preparations 247
    Method of staining 247
    Drawings, photographs and microphotographs 248

Systematic position of *P. impexus* 248
    Adult 248
    Larva 249

Distribution and specificity of *P. impexus* 251

Biology 252
    Adult 252
    Egg and oviposition period 255
        a. Time and place of oviposition 255
        b. Fecundity 256
        c. Development of the eggs 256
        d. Vitality and mortality of the eggs 257
        e. The egg and its hatching 257
    Larval development 258
        a. The first-instar larva 258
        b. The second-instar larva 259
        c. The third-instar larva 259
        d. The mature larva 260
        e. General considerations on the larval stages 262
    Prepupa and pupa 263
    General considerations on the life cycle of *P. impexus* in Switzerland and in Germany 263

Factors limiting the development of the population of *P. impexus* 264
    Scymnophagus mesnili 264
        a. Description by Dr. Ch. Ferrière 264
        b. Source of the material 265
        c. Life history of *S. mesnili* 265

---

* European Investigations.

PAGE
Centistes scymni 267
a. Description by Dr. Ch. Ferrière 267
b. Source of the material 267
c. Life history of the parasite 268
d. Effect of the parasite and reaction of the host 268
Gregarines 270
a. Source of the material 270
b. Notes on the life history and morphology of the known stages ... 270
c. Effects on the host and number of gregarines 271
Nematodes 271
Predators of *P. impexus* 271
Estimate of the value of *P. impexus* as a controlling agent 272
Rearing of *P. impexus* and shipment to Canada 272
General plan of the work 272
Rearing cage 273
Shipping box 274
Summary 275
Acknowledgements 275
References 276

Introduction.

The study of the biotic factors causing mortality among the Balsam Woolly Aphid, *Adelges piceae* (Ratz.),* in Canada was first undertaken between 1932 and 1934 at Fredericton, New Brunswick, about 30 years after the introduction of the Aphid into Nova Scotia (Balch, 1952). None of the native Canadian predators indicated by Balch seems to be present in Europe.

In 1933, *Leucopis* (*Leucopomyia*) *obscura* Hal. (Diptera, CHAMAEMYIIDAE) was introduced into Canada and 2,000 adults were liberated in New Brunswick. According to Balch " within a period of 14 years the insect has spread more than 150 miles from the nearest point of liberation and this establishes a remarkable case of rapid dispersal and successful establishment ". From 1935 to 1937 the following three additional predators were introduced from England to Canada, *Exochomus quadripustulatus* (L.) (Coleoptera, COCCINELLIDAE), *Hemerobius nitidulus* F. and *H. stigma* Steph. (Neuroptera, HEMEROBIIDAE). None of these latter species survived the severe winter climate. In 1950, the Commonwealth Institute of Biological Control, at the request of the Canada Department of Agriculture, initiated a study of the natural control agents of *A. piceae* in Europe in areas climatically most similar to eastern Canada. The study areas were established in eastern Switzerland, in southern Germany and in the Vosges area of France. In 1951 and 1952 it was possible to rear and ship to Canada *Pullus impexus* (Muls.), *Aphidecta obliterata* (L.) (Coleoptera, COCCINELLIDAE), *Laricobius erichsonii* Rosenh. (Coleoptera, DERODONTIDAE) and *Cremifania nigrocellulata* Cz. (Diptera, CHAMAEMYIIDAE) in the adult stage.

The purpose of the present study was to accumulate information on the natural enemies of *A. piceae* with special reference to the biology and habits of *P. impexus* and its parasite complex.

One hundred years have passed since the original description of the species *impexus* (Mulsant, 1850) was made. This species was referred to as predacious upon *A. piceae* by Komarek and Pfeffer in 1937 (Hofmann, 1938). Other entomologists who found *P. impexus* in the forest (Weise, 1884; Baudi, 1889;

---

* Annand (1928) arranged the species of the ADELGINAE under *Adelges* and *Pineus*, and the Genus *Dreyfusia* (Börner, 1952) was therefore included in the Genus *Adelges*. This arrangement is followed here.

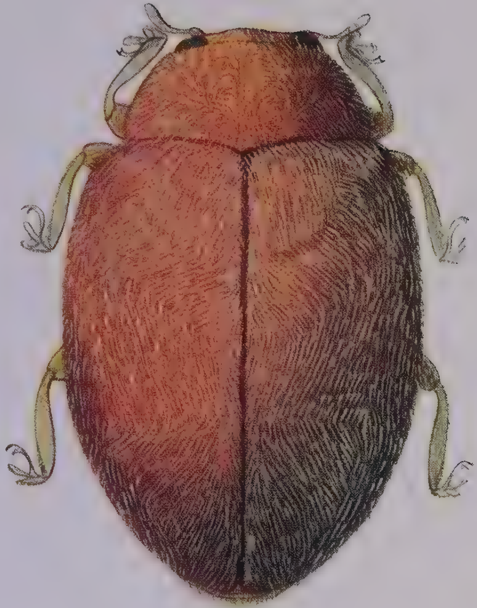


FIG. 1. *Pullus impexus* (Muls.), dorsal view.

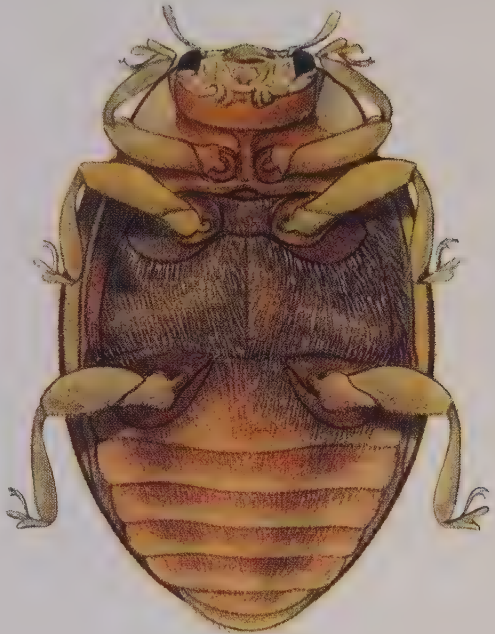
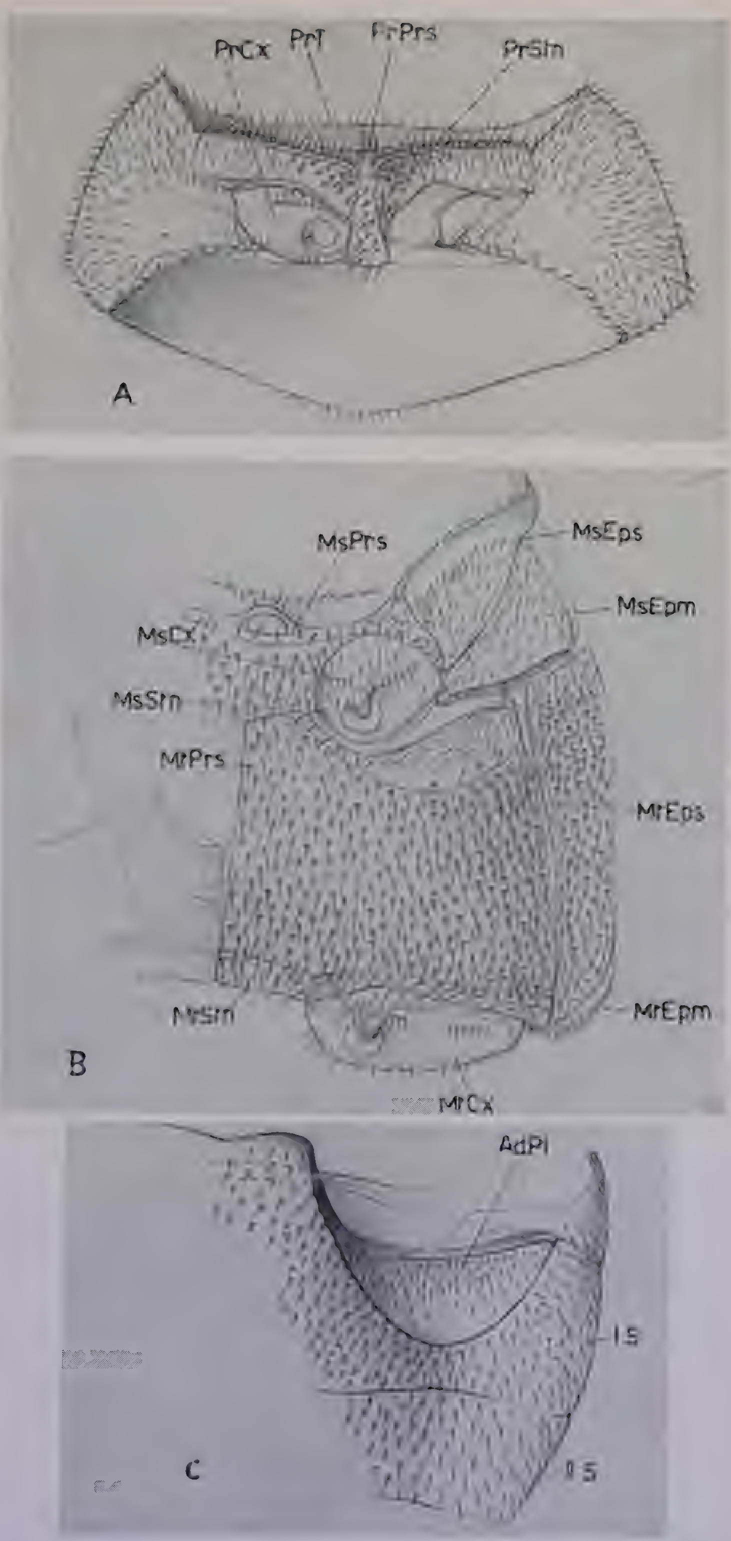


FIG. 2. *P. impexus* (Muls.), ventral view.


PrCx
PrT
PrPrs
PrStn
A
MsPrs
MsEps
MsEpm
MsCx
MsStn
MtPrs
MtEps
MtStn
MtEpm
B
MtCx
AdPl
I S
C
II S

A, prothorax and B, pterothorax of *P. impexus*, ventral view: *PrCx*, *MsCx*, *MtCx*, pro-, meso-, metacoxa; *PrT*, protergite; *PrPrs*, *MsPrs*, *MtPrs*, pro-, meso-, meta-presternum; *PrStn*, *MsStn*, *MtStn*, pro-, meso-, metasternum; *MsEps*, *MtEps*, meso-, meta-episternum; *MsEpm*, *MtEpm*, meso-, meta-epimeron. C, abdominal plate of the first abdominal sternite of adult of *P. impexus: AdPl*, abdominal plate; I S, II S, first and second

Schatzmayr, 1943; etc.) have not recorded the host upon which the Coccinellid feeds.

Three years' observations on the problem of *A. piceae* indicate that in general the most important predators comprise at most ten species (fig. 1). Three of these belong to the Coleoptera:

Pullus impexus (Muls.) (Coccinellidae)
Aphidecta obliterata (L.) (Coccinellidae)
Laricobius erichsoni Rosenh. (Derodontidae),

six to the Diptera:

Leucopis (*Leucopomyia*) *obscura* Hal. (Chamaemyiidae)
Leucopis griseola (Fall.) (Chamaemyiidae)
Cremifania nigrocellulata Cz. (Chamaemyiidae)
Cnemodon latitarsis Egg. (Syrphidae)
Syrphus arcuatus (Fall.) (Syrphidae)
Aphidoletes thompsoni Moehn (Cecidomyiidae)

and one to the Neuroptera:

Chrysopa ventralis Curt. (Chrysopidae).

In the spring, during the oviposition period of the Aphid, all ten species are present. *Aphidoletes thompsoni* is the first to make its appearance; the adults were noticed in 1951 on 23rd March (at Seegraeben). In April the adults of *Pullus impexus* leave their wintering places and in addition the larvae hatch from the eggs deposited the preceding autumn. At the same time *Laricobius erichsoni* is depositing its eggs in the Aphid brood; also during this period the first generation larvae of *A. thompsoni*, the hibernated larvae and pupae of *Leucopomyia obscura* as well as the larvae of *Chrysopa ventralis* are present. In May, when the oviposition by *Adelges piceae* reaches its peak and the trees are densely covered with white wax, the adults of all the other above-mentioned predators appear and deposit their eggs in the Aphid population. In May, therefore, the larval stages of all ten predatory species are present on the infested bark. Then the *Aphidoletes* produces its second generation and the larvae of Coleoptera and other Diptera develop into pupae. In June, when the population of *Adelges piceae* is heavily decimated by the predators, the adults of the new generation of *P. impexus* and of *L. erichsonii* are found on the trees. Among the wax remains, a few larvae of *Syrphus arcuatus* of the second generation, larvae of *Leucopomyia* and *Aphidoletes* (present in varying numbers until autumn) are roving about, and *Aphidecta* and *Chrysopa* adults emerge.

At this time a dispersion of some of the predacious species is noticed, and a slowing down of the activity of the remaining species to coincide with the end of the first host generation. It is quite obvious that successive waves of predators disorganise the *Adelges* population on the infested trunks. This is evidenced by the disturbed condition of the wax and wool secreted by the Aphids. From June to August the activity of the predators is continued by *Leucopomyia obscura* and *Aphidoletes thompsoni*, although even this is almost imperceptible. Other species, if present, are of no numerical significance.

The autumn generation of the *Adelges* begins with oviposition in August. A thin white wax layer again collects on the trunks among the greyish wax remains of the spring generation or on the trees newly attacked by the Aphid. At this time some of the predators resume their activity. The *Cremifania* adults emerge (first generation), a few *Syrphus arcuatus* show themselves, and *Aphidoletes*, *Leucopomyia* and *Cremifania* (second generation) increase rapidly. The adults of *P. impexus* are frequently observed and begin oviposition. Some *Cnemodon* are noticed as well as the first small larvae of *Chrysopa ventralis*. The components of the predator community on the autumn Aphid generation has changed slightly. There are neither thousands of Coleopterous larvae nor hundreds of Syrphid larvae and no particular disorder of the wool, as in the spring generation, is noticed.

Between the very small larvae of the three Diptera (*Aphidoletes*, *Leucopomyia* and *Cremifania*) and the Aphid there appears an orderly struggle, which almost escapes our notice. The intensity of the autumn Aphid generation depends, for the most part, upon the number of survivors remaining after the destructive action of the predator community on the spring generation. The three Coleoptera and *Syrphus arcuatus* are generally numerous on the spring infestation of the Aphid, whereas *Cremifania*, *Leucopomyia* and *Aphidoletes* reach their greatest numbers in the autumn. However, it is the combined activity of all the predator species in May that is responsible for the reduction of *Adelges* to a low level.

Each predator possesses one or more parasites (fig. 1) and some predators are affected with disease organisms causing at times serious mortality in their populations.

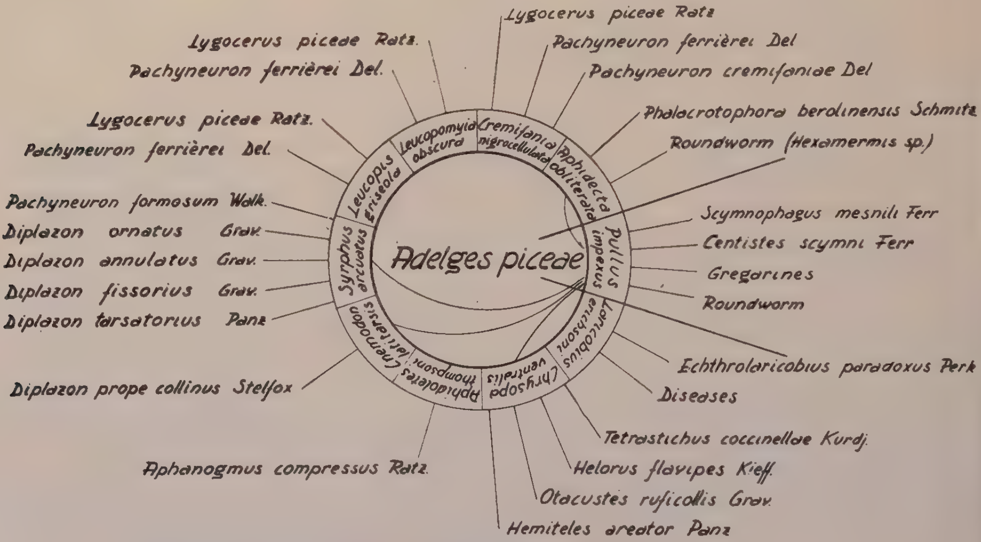

Lygocerus piceae Ratz.
Pachyneuron ferrièrei Del.
Lygocerus piceae Ratz.
Pachyneuron ferrièrei Del.
Pachyneuron formosum Walk.
Diplazon ornatus Grav.
Diplazon annulatus Grav.
Diplazon fissorius Grav.
Diplazon tarsatorius Panz
Diplazon prope collinus Stelfox
Aphanogmus compressus Ratz.
Lygocerus piceae Ratz
Pachyneuron ferrièrei Del
Pachyneuron cremifaniae Del
Phalacrotophora berolinensis Schmitz
Roundworm (Hexamermis sp.)
Scymnophagus mesnili Ferr
Centistes scymni Ferr
Gregarines
Roundworm
Echthrolaricobius paradoxus Perk
Diseases
Tetrastichus coccinellae Kurdj.
Helorus flavipes Kieff.
Otacustes ruficollis Grav.
Hemiteles areator Panz
Adelges piceae
Leucopomyia obscura
Cremifania nigrocellulata
Aphidecta obliterata
Pullus impexus
Laricobius erichsoni
Chrysopa ventralis
Aphidoletes thompsoni
Cnemodon latitarsis
Syrphus arcuatus
Leucopis griseola

Fig. 1.—The predators of *Adelges piceae* and their parasite complex.

To the above predator community, forming the basis for biological control of the Aphid, we may add some occasional predators which, either isolated or with a life-cycle not coinciding with that of the host, have little or no importance in the destruction of the *Adelges*. Among those most often encountered were:

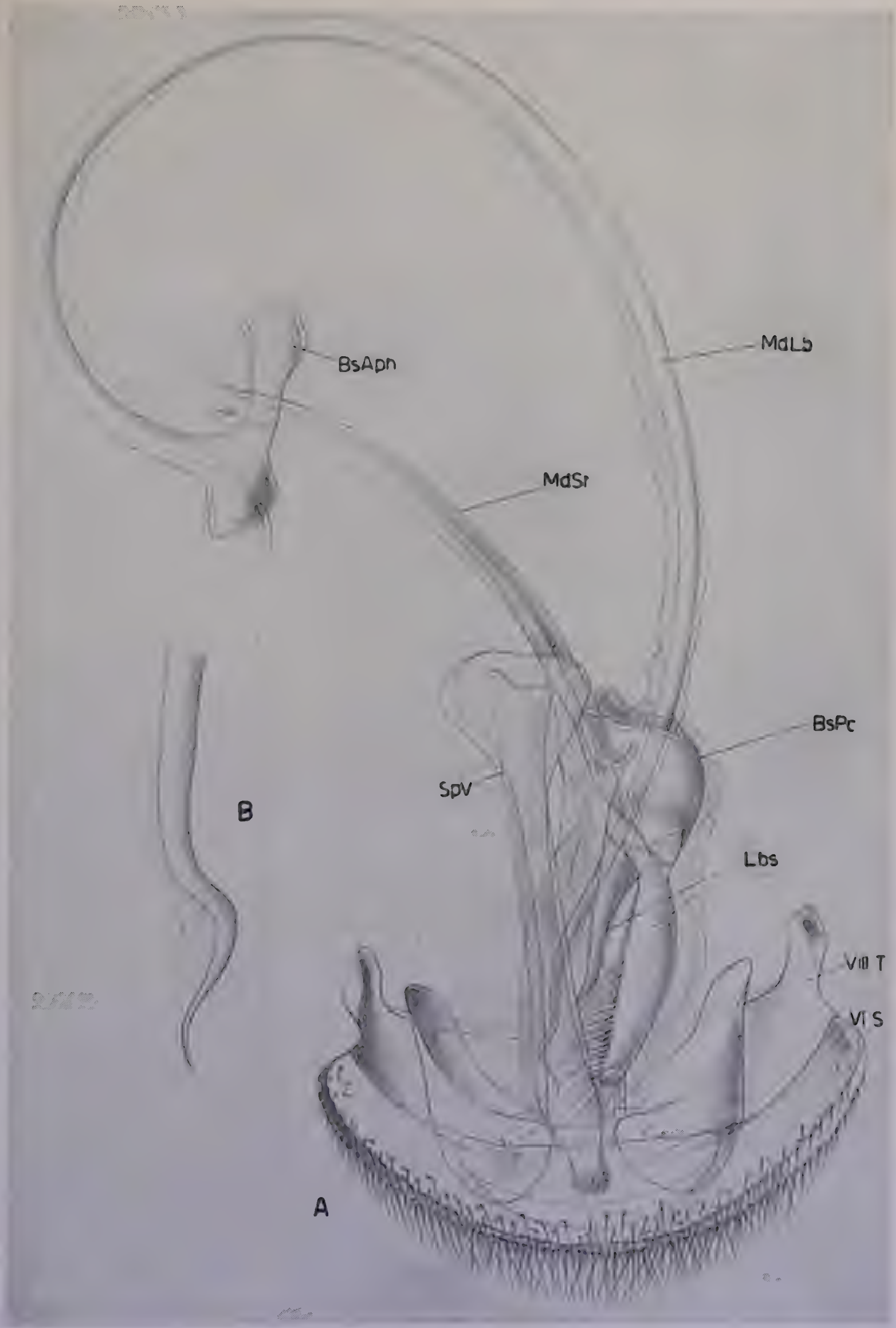
Anatis ocellata (L.) (Coleoptera, COCCINELLIDAE)
Neomysia oblongoguttata (L.) ,, ,,
Propylea 14-punctata (L.) ,, ,,
Exochomus 4-pustulatus (L.) ,, ,,
Coccinella 7-punctata L. ,, ,,
Epistrophe balteata (Deg.) (Diptera, SYRPHIDAE)
Raphidia sp. (Neuroptera, RAPHIDIIDAE)
Triphleps sp. (Hemiptera, ANTHOCORIDAE).

In addition to the insects some Mollusca such as *Limax maximus* L. and *L. tenellus* Nilss. were found by Dr. Wichmann at Munich. Mites are also recorded, among which *Lephthyphantes obscurus* Blackwall is stated by Dr. Wichmann to be most frequent.

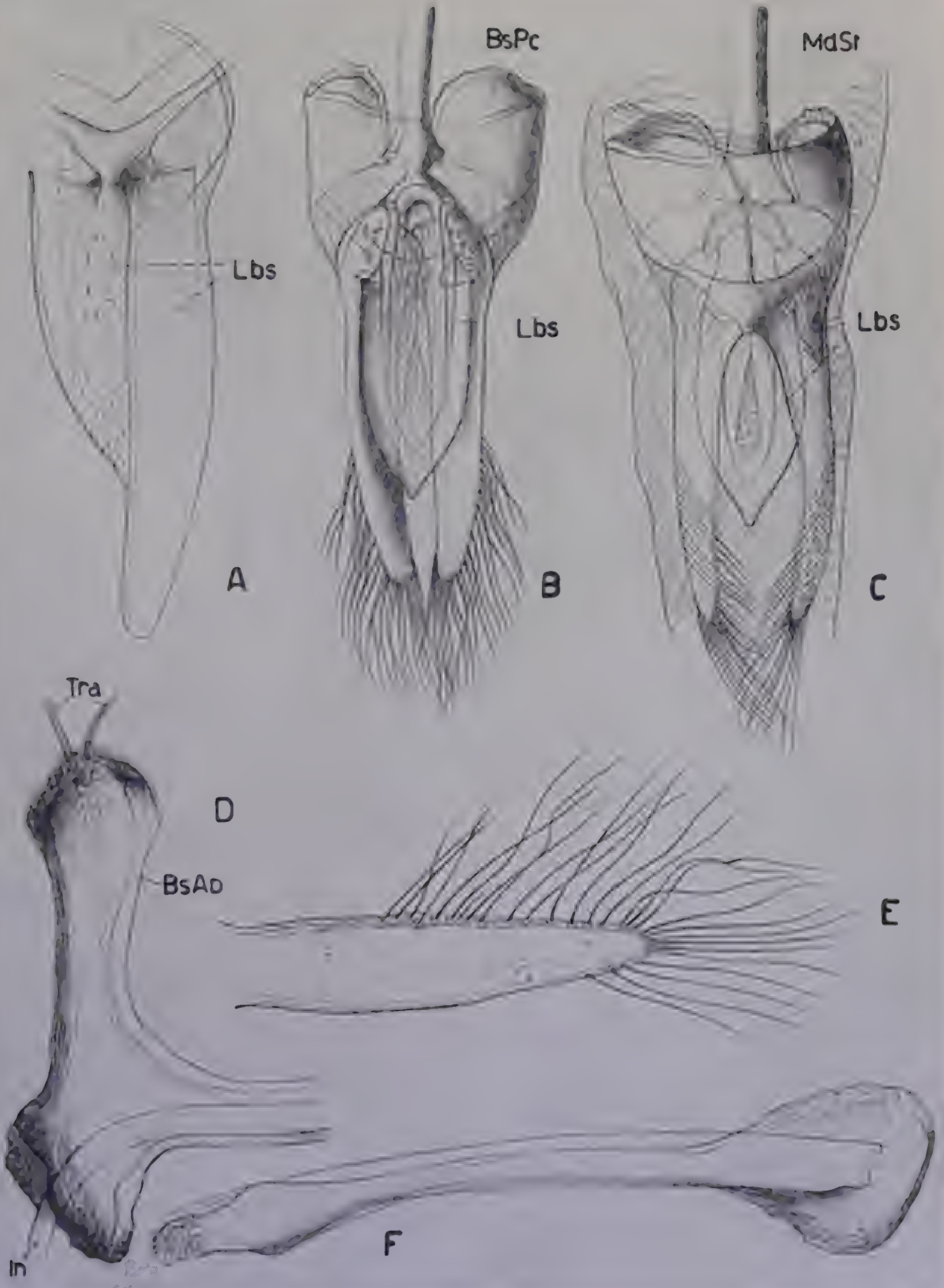
Method of Rearing and Techniques employed in the Study of *Pullus impexus.*

Rearing in the laboratory.

The predators reared on bark infested with *A. piceae* in petri dishes, open or covered with organdie, or containing moist cotton or earth, always suffered a


BsApn
MdLb
MdSr
BsPc
SpV
B
Lbs
VIII T
VI S
A

Male genitalia of *P. impexus:* A, ventral view of the genitalia; B, virga: *BsAph*, basal apophysis; *MdSt*, median strut; *MdLb*, median lobe; *BsPc*, basal piece; *Lbs*, basal and lateral lobes; *SpV*, spicula ventralis; VIII T, 8th tergite; VI S, 6th sternite.



Parts of the male genitalia of *P. impexus:* A, basal and lateral ventral lobes, schema; B, C, latero-internal, latero-external view of the tegmen; D, basal apophysis; E, a lateral lobe of the tegmen; F, spicula ventralis: *Lbs*, basal and lateral lobes; *BsPc*, basal piece; *MdSt*, median strut; *BsAph*, basal apophysis; *Tra*, trachea; *In*, intima of the ductus

rather heavy mortality. This was chiefly due to the growth of mould on the bark surface. Therefore an attempt was made to simulate the natural conditions. The data supplied by a small meteorological station established on the Pfannenstiel (Zurich) in an *Adelges* infestation were utilised.

In studying the problem of *Adelges* a method was adopted which had already been successfully employed by Prof. L. P. Mesnil in rearing parasites of *Carulaspis visci* (Schr.) on *Juniperus communis* L. Pieces of bark, freshly detached from the infested trees were introduced into tubes 4 cm. in diameter and 20 cm. in length. Through these tubes an air flow which could be regulated was directed. The tubes were exposed to room temperature, which remained more or less constant in the laboratory during rearing. Two important details were considered, the relative humidity control to prevent the bark from drying too rapidly, and the air flow control to prevent mould from forming. In the winter, the material was exposed to the natural conditions in the forest in the Pfannenstiel area. With this method there was no mortality in rearing *P. impexus.*

Fixation of the material.

For the fixation of the material, alcoholic Bouin (Langeron, 1949) was used exclusively with excellent results. After having slit the insects open laterally to allow the fixative to penetrate the body rapidly and uniformly they were left in alcoholic Bouin for 48 hours. Then the material was washed frequently in 80 per cent. alcohol until any trace of the picric acid had disappeared. It was then placed in small labelled tubes containing 80 per cent. alcohol and stored in large jars.

Microscopic preparations.

Generally, special oculist's bistouries were used for dissections under the binocular microscope. For histological studies the microtome was used, *e.g.*, in the study of the Gregarines. For paraffin inclusions the object was passed through the dehydration series in alcohol (two baths in absolute alcohol) and then to xylol. The material was left for 24 hours in a methylbenzoate bath containing 1 per cent. of celloidin; afterwards through three successive toluol baths within 24 hours, and finally into paraffin M.P. 52°–54°. The object was left in the paraffin for four to five days at a temperature of 58°C. For the study of sclerotised parts 10 per cent. potassium hydroxide was used.

Methods of staining.

The sclerotised parts, cleared with potassium hydroxide, were stained with basic fuchsin in absolute alcohol and mounted in Canada balsam. For the staining of organs of relatively large size (heart, pericardial cells, muscles, etc.) the Mann biacid technique was used (Langeron, 1949) replacing eosin with xilidin ponceau, and differentiating simply in 80 per cent. alcohol after washing in distilled water. For histological staining and for staining of very small entire organs (salivary glands) the modified method of Dominici (Langeron, 1949) was used. The organs and the microtome sections after having passed through the xylol and alcohol series, were washed in distilled water, then left 15 minutes in a solution composed of 1 per cent. erythrosin blue and 1 per cent. xilidin ponceau. After two washings in distilled water, they were stained with 0·1 per cent. toluidin blue solution until the object assumed a violaceous shade. This is one of the most critical moments in staining, because too deep toluidin staining may ruin the differentiation process. Both staining and differentiation must be performed beneath the binocular microscope. For this reason it is advisable to glue the microtome sections on the glass slides and to handle them in strongly concave watch glasses of 5 cm. diameter. From the toluidin the sections are passed to distilled water, then to differentiation in 80 per cent. alcohol, to a rapid dehydration, to xylol and mounting in Caedax. The Caedax, made in Germany, has taken the place of Canada balsam, because in the latter the staining loses its freshness with time.

Drawings, photographs and microphotographs.

The most satisfactory drawings were made on Sihl Superbus cardboard 540 gr. with Wolff's carbon drawing pencils (HH, H, HB and BBB) together with water colours for coloured plates. They were drawn with the use of the Leitz stereoscopic binocular with Leitz camera lucida or with Leitz microscope with double iris. For the coloured plates of the two Hymenopterous parasites of *P. impexus* a Leitz Ultropak with "Relief Kondensor" adapted to the microscope was employed. Nearly all the *P. impexus* photographs were taken in the laboratory with a Leitz camera using photographic plates. For microphotographs an Exakta-Varex camera adapted to the Leitz monocular microscope was used.

Systematic Position of *P. impexus*.

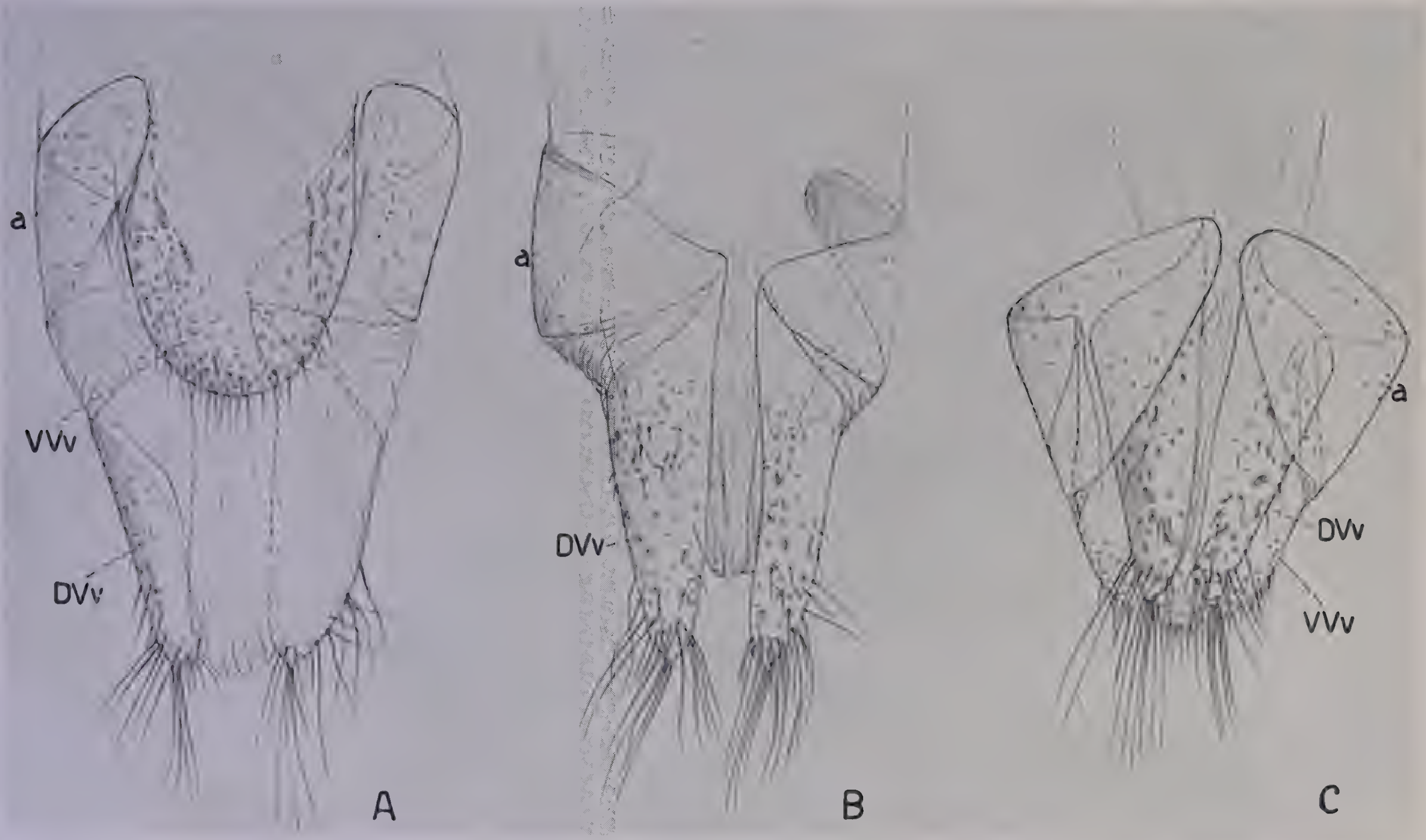
Adult.

P. impexus (Coccinellidae, Coccinellinae) (Pl. XI, figs. 1 & 2) belongs to the well known tribe Scymnini, including insects which—with very few exceptions—are predators of Coccidae, Aphididae, Aleurodidae, Thysanoptera and mites. The genus *Scymnus* Kugelann *s.l.* includes a great number of species generally of small size, sometimes difficult to determine and has been subdivided by Mulsant and Weise (Reitter, 1911) into subgenera, with a particular view to the marginal outline of the prosternal carinae and to the form of the abdominal plates (metacoxal lines) at the sides of the first abdominal sternite; the species *impexus* belongs to the subgenus *Pullus*. Later authors (Kuhnt, 1913; Schaufuss, 1916; Capra, 1927; etc.) accorded generic status to *Pullus*. The generic characters separating *Pullus* from the other genera of the tribe Scymnini are reproduced in Plate XII, and do not require special explanations.

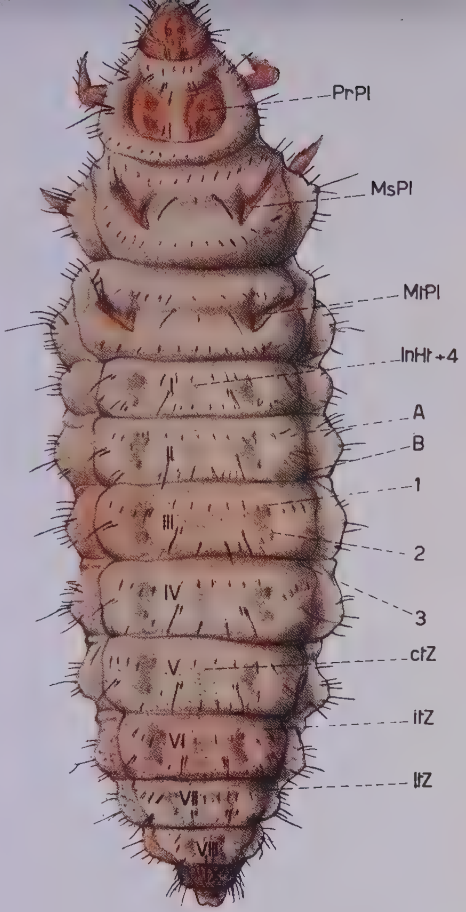
Schilder and Schilder (1928) pointed out the necessity of correlating the genus with the particular diet of the different species. The species attributed to the genus *Pullus* feed particularly on Aphididae, but not every species of specific Aphid predators are included in the genus *Pullus*. From the systematic standpoint, constant characters for the separation of the genera *Pullus* Muls. and *Scymnus* Kugelann *s.str.* have not yet been found. The species *impexus* is a predator of *A. piceae* and in the present work it is placed in the genus *Pullus*.

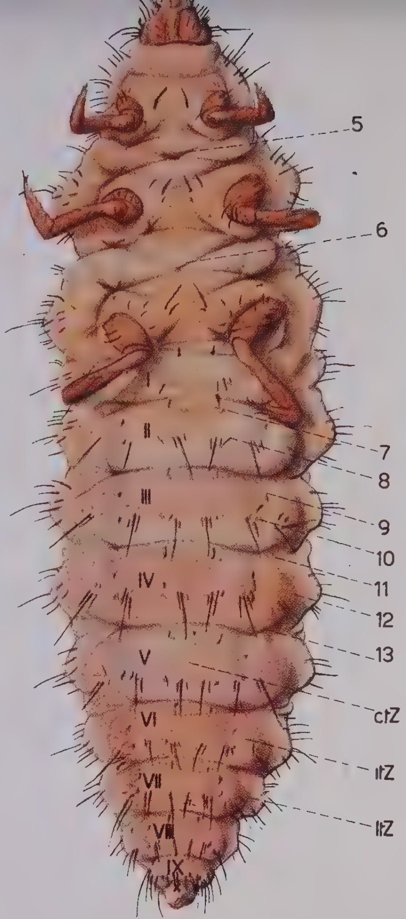
P. impexus is distinguished from the congeneric species and especially from *Scymnus abietis* (Payk.) by the peculiar varying hair direction on the elytra. Anteriorly, near the median body line, this thin light brown, almost yellow, pilosity (Pl. XI, fig. 1) is directed, at first more or less longitudinally, slightly towards the external margin of the wing, then strongly outwards. On the central part of the elytra the pilosity is directed again towards the median line, then it turns outwards on the posterior part of the wing. Along the external posterior margin of the wing, almost at the level with the penultimate abdominal tergite, the lateral pilosity is directed towards the median line, meets with the externally directed one and follows the longitudinal direction as far as the end of the wing. The hairs on the elytra of *P. impexus* are relatively long. The body is oval in shape, one and a half times longer than broad, with a total length of 2–2·3 mm. The colour is uniformly light brown, sometimes dark brown on the meso- and metasternites and partially on the first abdominal sternite.

To supplement possible systematic studies, the genitalia of both of male and female are described. *Male* (Pls. XIII, XIV): The genitalia open between the 8th


a
VVv
DVv
A
a
DVv
B
a
DVv
VVv
C

Female genitalia of *P. impexus:* A, ventral view; B, C, dorsal view; *DVv*, dorsal valve, *VVv*, ventral valve; *a*, superior part of the dorsal valve.


PrPl
MsPl
MtPl
InHt+4
A
B
1
2
3
ctZ
itZ
ltZ
II
III
IV
V
VI
VII
VIII


5
6
7
8
9
10
11
12
13
ctZ
itZ
ltZ
II
III
IV
V
VI
VII
VIII
IX

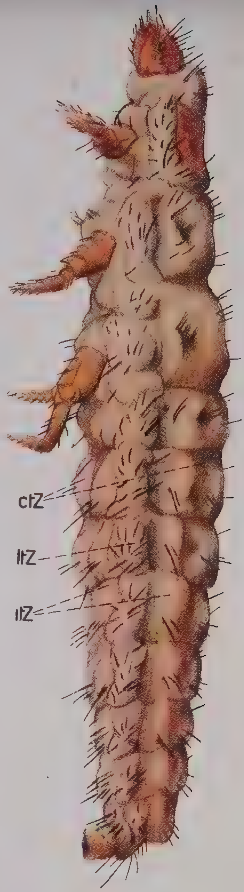


FIG. 1. *P. impexus*, 4th-instar larva, dorsal view: *PrPl*, *MsPl*, *MtPl*, pro-, meso-, metathoracic plates; *InHt* + 4, attachment of the cone-shaped portion of the heart-ostium + insertion of the median external dorsal muscles; 1, 2, 3, insertion of muscles, see text fig. 2; A, B, insertions of lateral muscles; *ctZ*, *itZ*, *ltZ*, central, intermediate, lateral zones of the body;

FIG. 2. *P. impexus*, 4th-instar larva, ventral view: 5, 6, muscle complex of the sternal thoracic region, attachment to the skin; 7, 8, 9, 10, 13, insertion of muscles, see text fig. 2; 11, 12, insertion of lateral muscles.

FIG 3. *P. impexus*, 4th-instar larva, lateral view: *ctZ*, *itZ*, *ltZ*, central, intermediate, lateral zones of the larval body.

tergite and the 6th sternite of the abdomen, below the digestive tract. The tergite as well as the sternite is provided with terminal bristles, the latter also with groups of supposed sensilla distributed near the bristles along its posterior margin. The 7th and 8th sternite form a single sclerite situated between the 8th tergite and the 6th sternite. The spicula ventralis constitutes the 9th sternite of a segment of which the tergite has a special form (Pl. XIII); it is laterally elongated and situated below the 8th. The median lobe receives at its base the ductus ejaculatorius which is strongly arched and passes through the basal piece. The basal piece forms a sort of ring closed at its base by the median strut. The basal piece bears three appendages, the basal and lateral lobes; the lateral lobes are more external, elongated, with marginal bristles, whereas the basal one is more internal and has the form of a pointed spade. It has no bristles but seems to be well provided with nerve endings. These appendages are extruded during the act of copulation. The basal piece, basal and lateral lobes together form the tegmen (Wilson, 1927). *Female* (Pl. XV): the genitalia are very simple, composed of a rounded ventral valve with the terminal portion well chitinised, and by two dorsal valves. These valves are posteriorly elongated like the two lateral lobes of the male and anteriorly (a) widened and join the sides of the ventral valves ventrally. The two parts of the dorsal valves are joined by a membrane, except at the median dorsal point. This membrane allows the anterior part of the dorsal valves (a) to descend on the posterior one when the insect is resting (C). The ventral valve and the posterior part of the dorsal valves are provided with bristles and groups of sensilla. On the anterior part of the dorsal valves are isolated sensilla only.

Larva.

The morphological characters of the Scymnid larvae used in van Emden's keys (1949) allow us to arrive at the genus *Scymnus s.l.* but not at the genus *Pullus* Muls. (subgenus in van Emden's keys); in the work of van Emden the species *impexus* Muls. is not mentioned. For the determination of the larvae of *P. impexus* as many details as possible have been set out and some are illustrated in fig. 2 and Plates XVI–XIX. The characters described are common to the four larval instars; thus the mature larva only will be considered.

The fourth-instar larva (Pl. XVI, figs. 1, 2, 3) is 4–5 mm. in length; its maximum width does not exceed 1·5 mm. The larva is rather flat and the body fusiform. The head is very small and slightly sunken into the thorax. The thorax is a little more than a third of the total body length. In nature the mature larva is covered with wax, as are the other larval stages, and appears as a white mass in which it is possible to distinguish both the thoracic segments and the first abdominal ones. With the wax removed, the mature larva is dark orange with a much deeper pigmentation than that found in the first stage larva. The head (Pl. XVII), the thoracic tergal plates (Pl. XIX), the tergum of the penultimate segment and part of the anal segment (Pl. XIX), the legs and points of insertion of the muscles on the skin are brown.

Both dorsally (Pl. XVI, fig. 1) and ventrally (Pl. XVI, fig. 2) the body is divided into three longitudinal zones well defined by the muscular system. The muscular system causes numerous folds which are particularly accentuated on the side of the body and on the sternal thoracic region. The central longitudinal zone (ctZ) is defined between the segments of the thorax and of the abdomen by the large tergosternal muscle (3, Pl. XVI, fig. 1 & 3, text fig. 2; 13, Pl. XVI, fig. 2 & 13, text fig. 2) which limits the mesenteron laterally and the digestive system in general. The separation of the central zone from the intermediate one is marked on the abdominal segments by the points of insertion of two muscles on each tergite (1, 2, Pl. XVI, fig. 1 & 1, 2, text fig. 2) and sternite (9, 10, Pl. XVI, fig. 2 & 9, 10, text fig. 2). On the pro-, meso- and metathoracic tergites the central zone extends between the thoracic plates (Pl. XVI,

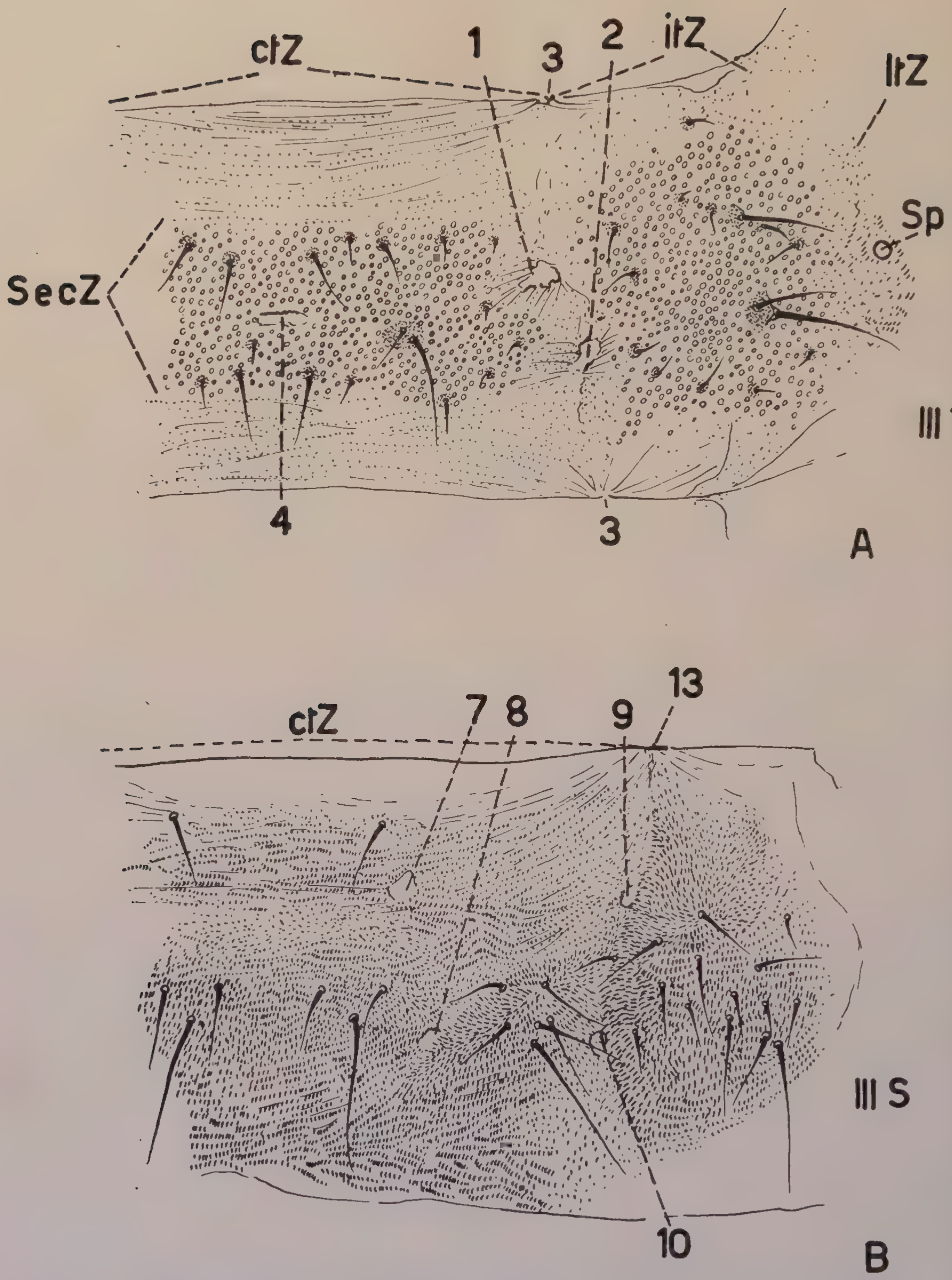
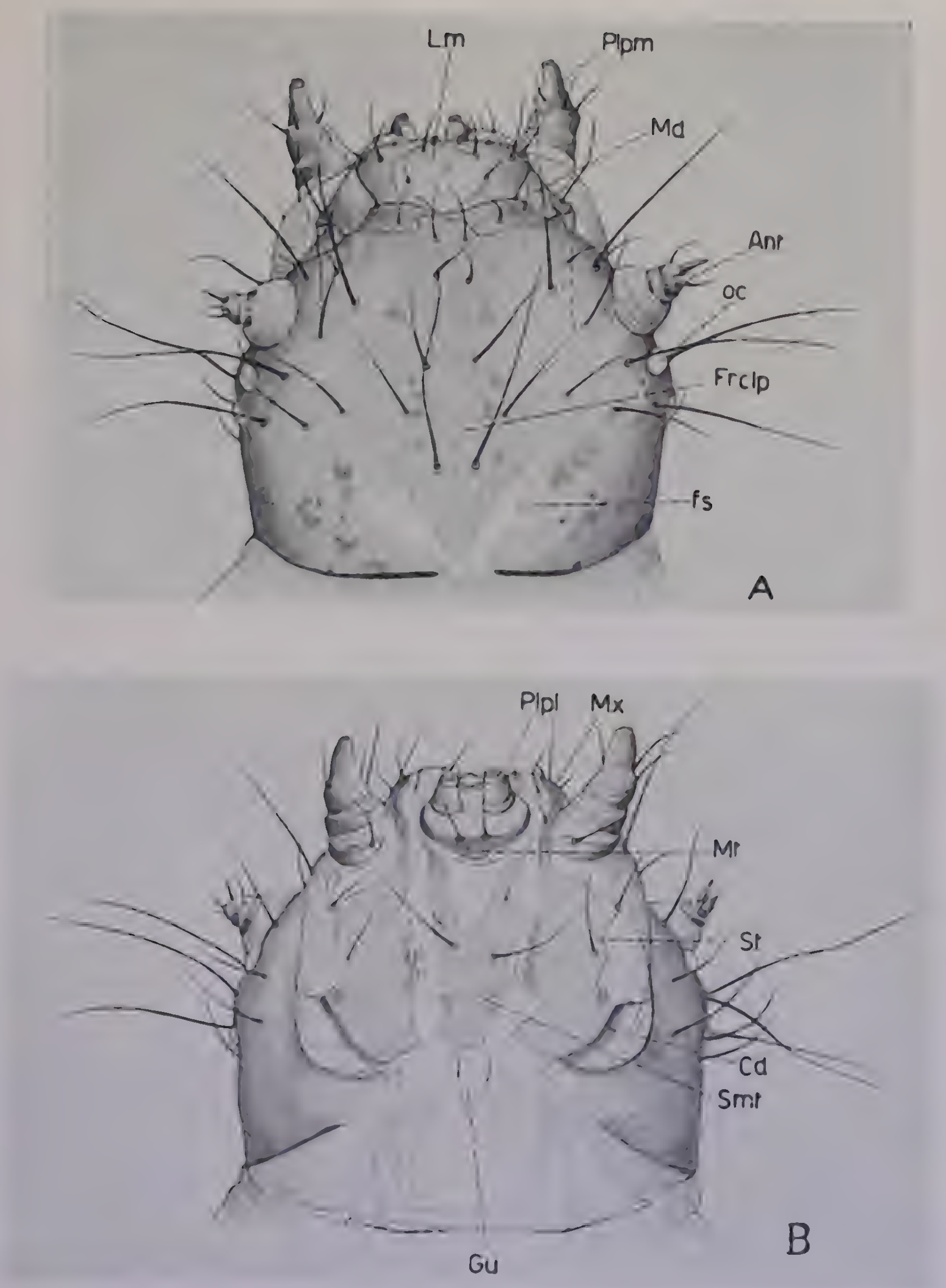
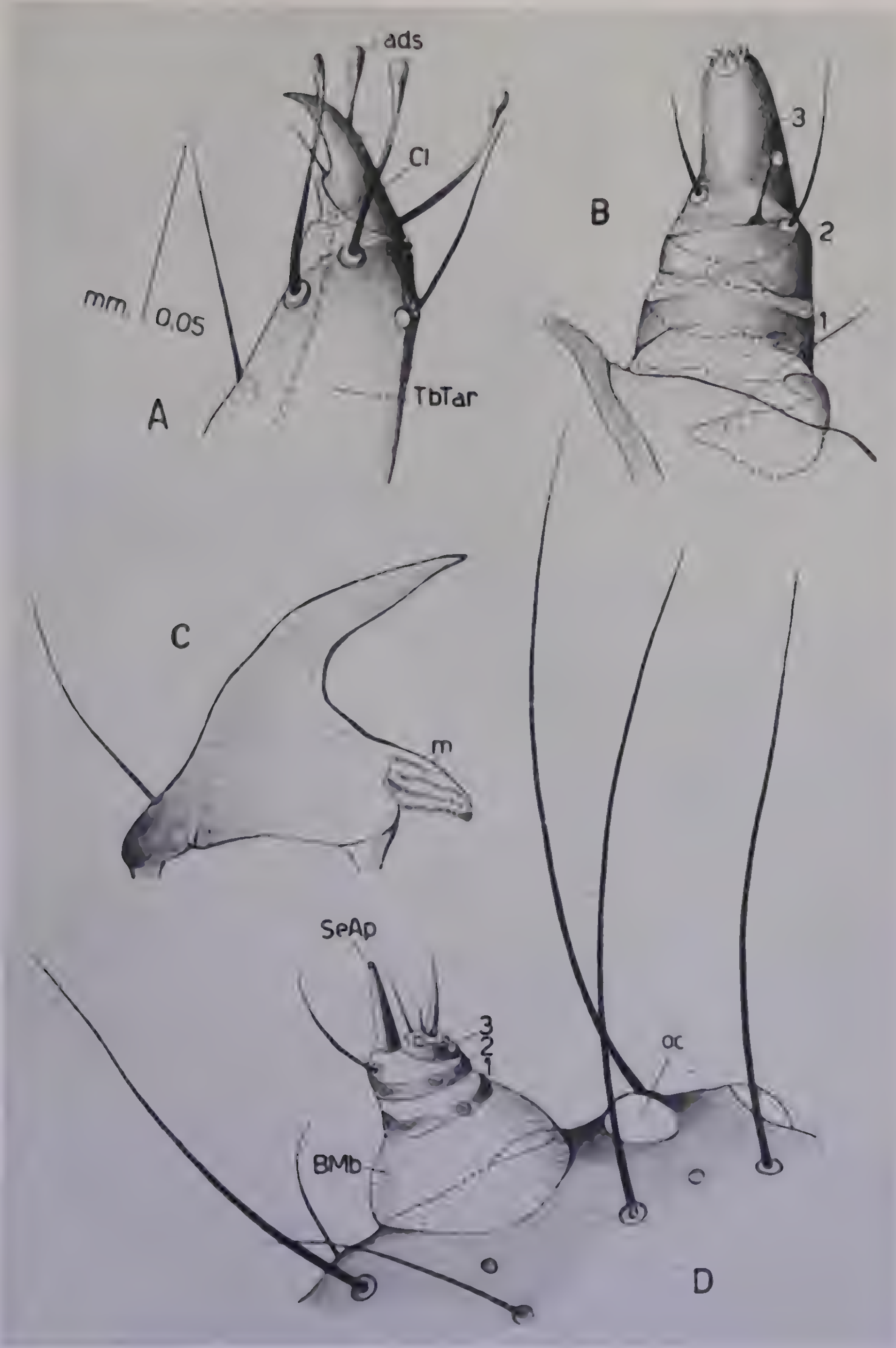


Fig. 2.—Muscle insertions and chaetotaxy on third abdominal tergite A, and sternite B, of fourth-instar larva of *P. impexus.* Insertion of muscles: 1, lateral external dorsal; 2, lateral; 3, tergosternal; 4, the two median external dorsals; 7, median external ventral; 8, lateral external ventral; 9, 10, lateral; 13, tergosternal. *SecZ*, zone of wax secretion; *ctZ*, *itZ*, *ltZ*, central, intermediate and lateral zones; *Sp*, spiracle; III T, III S, third tergite and third sternite of the abdomen.


Lm
Plpm
Md
Ant
oc
Frclp
fs
A
Plpl
Mx
Mt
St
Cd
Smt
B
Gu

Head of fourth-instar larva of *P. impexus:* A, dorsal view; B, ventral view: *Lm*, labrum; *Md*, mandible; *FrCpl*, fronto-clypeal area; *Plpm*, maxillary palpi; *Ant*, antenna; *Plpl*, labial palpi; *Mx*, maxillae; *Mt*, mentum; *St*, stipes; *Cd*, cardo; *Smt*, submentum; *Gu*, gula; *oc*, ocelli; *fs*, frontal suture.


ads
Cl
mm 0.05
TbTar
A
B
3
2
1
C
m
SeAp
3
2
1
BMb
oc
D

Fourth-instar larva of *P. impexus:* A, claw and adhesive setae, lateral view; B, maxillary palpus, dorsal view; C, mandible, dorsal view; D, antenna, dorsal view: *Cl*, claw; *ads*, adhesive setae; *TbTar*, tibio-tarsus; *m*, molar part of the mandible; *Bmb*, basal membrane; *SeAp*, sensorial appendage; *oc*, ocellus; 1, 2, 3, first, second and third sclerotised rings.

fig. 1 & Pl. XIX). On the abdominal tergite of this zone one can perceive a slight inflection of the skin in the centre of each segment. This inflection is caused by two small median external dorsal muscles arising from the posterior segmental suture and converging at the centre of the segment, and by the superior cone-shaped portion of the heart-ostium, the vertex of which is attached to the tergum (InHt + 4, Pl. XVI, fig. 1; 4, text fig. 2). On each abdominal sternite the two transverse folds result from the presence of two pairs of small (median and lateral external ventral) muscles also arising from the posterior margin of the segment.

The intermediate zone (itZ) is regular in all the tergites and in the abdominal sternites. It is separated from the lateral one by a very deep fold (A, B, Pl. XVI, fig. 1; 11, 12, Pl. XVI, fig. 2). The lateral zone (ltZ) and the sternal region of the thorax are folded the most. The points of attachment of the two ventral muscle complexes to the skin (5, 6, Pl. XVI, fig. 2) are evident in the thoracic sternal region.

The mesothoracic plates form an angle of about 45° with the median line whereas the metathoracic plates form a slightly wider angle (Pl. XIX).

The dorsal and dorsolateral strumae (fig. 2) are each provided with two setae, the smaller one set nearer the median body line. The frontal suture (Pl. XVII) is V-shaped, diverging to the base of the antennae where it becomes less distinct. The epicranial suture is absent. The apex of the mandibles is simple (Pl. XVIII). The molar part is prominent and in the shape of a process with hair-like asperities. The second segment of the labial palpi (Pl. XVII) is well developed, much longer than wide and conically truncate. The first segment is very short and ring-shaped. The antenna (Pl. XVIII) is evidently three-segmented, the second segment as long as the first. The sclerotised ring of the second segment of the maxillary palpi (Pl. XVIII) is about twice as long on the outer surface as on the inner one, twice as wide as long on the outer surface and much longer than that of the first segment.

It would be useful to look for other characters in the larva allowing a better definition of the several genera and the determination of species. Perhaps a detailed study of the head chaetotaxy of many related species would offer characters of systematic value.

Distribution and Specificity of *P. impexus*.

In the present work, carried out in Europe, the predator was always found in association with *Adelges piceae*. In Switzerland *P. impexus* was collected in large numbers at Seegraeben near Zurich in 1950 and 1951 and in smaller numbers on the Pfannenstiel, at Winterthur, Aathal, Ottenhausen, St. Gallen, Binz and Wil. At Aathal and Winterthur *P. impexus* was abundant in 1952 only and in Naenikon in 1950 only (spring). The predator was observed in France at Ribeauvillé (Ht. Rhin) by Mr. H. G. Wylie. In Germany it was observed in the south, particularly in Bavaria, by Dr. J. Franz. It is apparently absent from northern Germany since it was not found at Flensburg, near the Danish frontier, where our most northern observation point was located.

According to Korschefsky (1931) *P. impexus* has a wide distribution extending from central Europe to north Africa. Dr. F. Capra, of the Museum of Natural History, Genoa, states that *P. impexus* has been found in Piedmont (northern Italy), there being specimens in the museum from the following localities:—Val Sesia, 28.viii.1922 (F. Solari); Val Pesio (F. Baudi). Baudi (1889) states that *Scymnus abietis* Payk. may be found in quantity by beating the branches of *Abies pectinata* in the Maritime Alps, but Dr. Capra, upon re-examination of the Baudi collection, found *impexus* under the name of *abietis*, originating from Val Pesio. Therefore he indicates that the quotation from Baudi's catalogue refers partly at least to *P. impexus*. Luigioni (1929) found *impexus* in Italy in the Maritime Alps, Tuscany and Lazio. From Tuscany there are also specimens of the predator in the Museum of Natural History, Genoa, from the following localities:—near Pistoia, 1906 and 1922 (F. Solari); Mount Argentaro, 1907 (F. Solari); Vallombrosa, 1930 (A. Gagliardi). Two specimens of *impexus* were found by the author on 29th June 1952, in the *Abies alba* forest of Vallombrosa, where no infestation of *A. piceae* exists. Schatzmayr (1943) has collected *impexus* "in series" on Mount Pollino, on the boundary between Lucania and Calabria, in southern Italy. M. Rungs, of the Service for Plant Protection, Rabat (Morocco), states that *impexus* does not occur in the African region, where *A. piceae* does not exist and *Abies alba* is very rare. M. D'Aguilar, of the National Institute of Agricultural Research, Versailles, informed me that the *impexus* in the Gruardet collection were collected from the Vosges, and those in the Sicard collection from both the Vosges and the Basses-Alpes. Sainte-Claire Deville (1935–38) states that the Coccinellid is to be found in the Vosges, in the subalpine zone of the Basses-Alpes, in the Alpes-maritimes and also in the Pyrenees, especially on *Abies*. Dr. Beier, of the Museum of Natural History, Vienna, informed me that the *impexus* specimens in that Museum originated in Calabria (southern Italy), southern France, the environs of Vienna, from Maehren and also from Hungary.

Thus the distribution of *impexus* in Europe extends southward beyond that of *A. piceae*. In the southern regions of Europe the Coccinellid might have adapted itself to a diet different from the one observed in the present work in the more northerly regions of the Swiss Alps. This is supposition, however, for the exact distribution of the Aphid is not known with certainty. For this reason the degree of specificity of the predator is still unknown. Since in the areas studied *P. impexus* has been always found in the *Adelges piceae* infestations, it must be closely related to this host, due in part to the environment of the Aphid. In captivity *impexus* larvae develop normally on *A. nordmannianae* (Eckstein) (*nüsslini* (C.B.)) as well as on *A. piceae*, whereas in nature pure infestations of *A. nordmannianae* are always free from the predator.

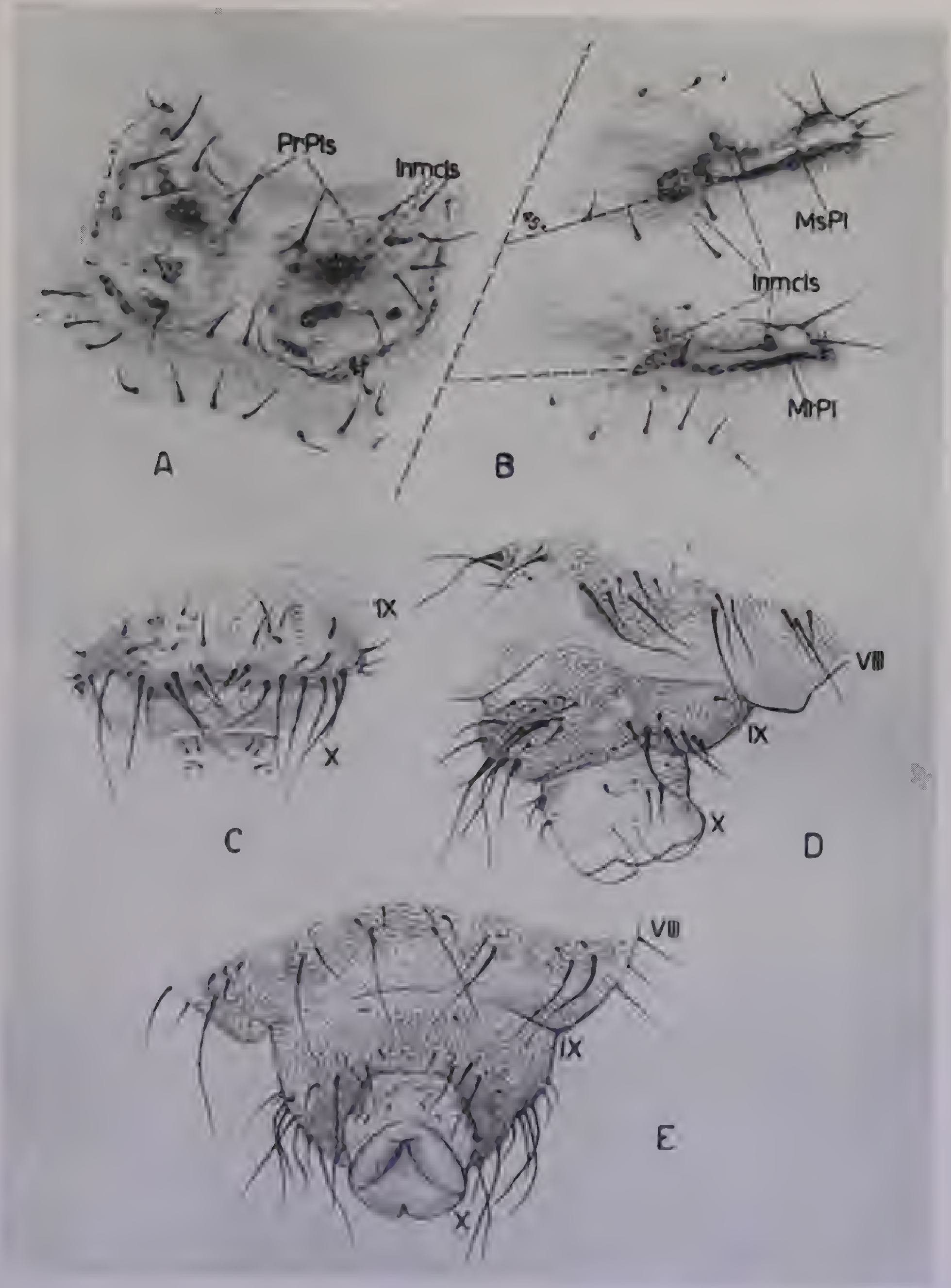
Biology.

Adult.

The longevity of *P. impexus* adults is estimated at 12–13 months. Individuals of the preceding generation are to be found until the end of June on the *Adelges* infestation together with the fresh adults emerging towards the end of May or during June. The adults of the old generation are generally recognisable by the darker colour of the thoracic and the first abdominal sternites.

The adults emerging at the end of May and beginning of June remain on the *Adelges* infestation (spring generation) which is starting to decline. By the beginning of July they are seen less frequently and during this month those remaining change their activity period and become crepuscular. During the day they remain hidden, possibly due to the rather high temperature (28–30°C.). In this period copulation either does not take place or is very rare, and activity is restricted to feeding. At this time the ovaries are developing and maturing in preparation for oviposition in August.

The autumn generation of *Adelges* appears rapidly in August and within a week may change the aspect of the infestation area, as it did at Seegraeben in 1950. Coincident with this rapid increase in the *Adelges* population is the gradual increase in numbers of the adult predators. Copulation occurs followed by heavy oviposition. The highest point of this threefold activity is attained in September (observations at Seegraeben, Pfannenstiel, Aathal and Winterthur). In early October, when the temperature is dropping, the adults gradually


PrPls
Inmcls
Inmcls
MsPl
Inmcls
MtPl
A
B
IX
X
C
VIII
IX
X
D
VIII
IX
E
X

Anatomical details of the larval body of *P. impexus:* A, plates of the prothorax, B, plates of meso- and metathorax; C, D, E, last abdominal segment, dorsal, lateral and ventral views; *PrPls*, prothoracic plates; *MsPl*, *MtPl*, meso- and metathoracic plates; *Inmcls*, insertion of the muscles; VIII, IX, X, 8th, 9th, 10th abdominal segments.

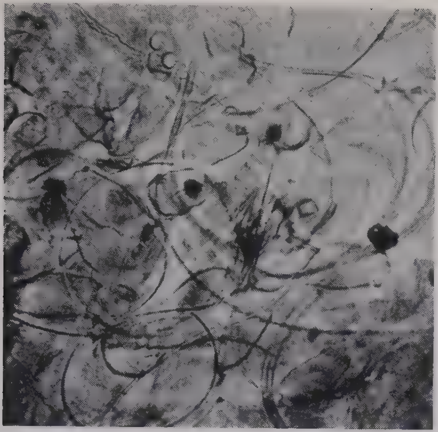


FIG. 1. Residues of sistentes found in the mesenteron of adults of *P. impexus*.

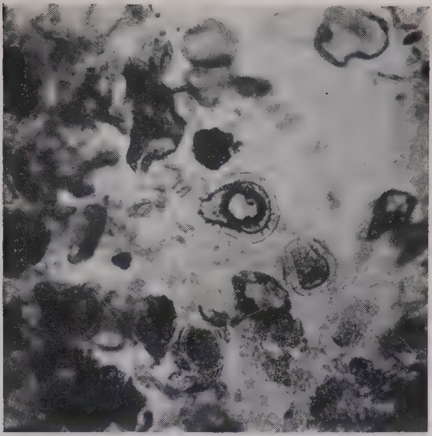


FIG. 2. Fungal spores from the mesenteron of adults of *P. impexus*.

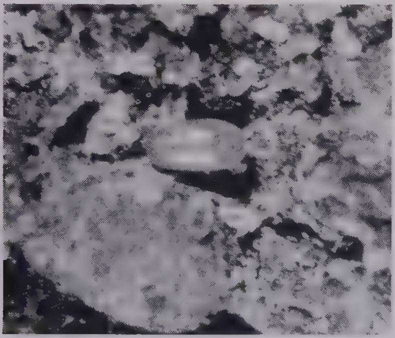


FIG. 3. Egg of *P. impexus* deposited in the *Adelges* wax of the spring generation at Naenikon in 1950.

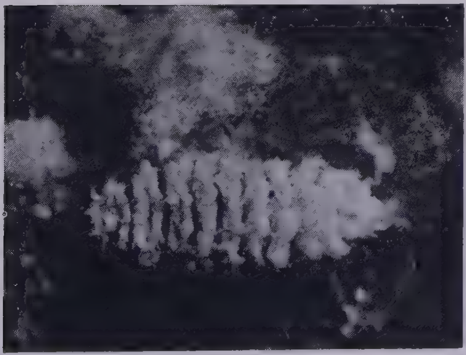


FIG. 4. Fourth-instar larva of *P. impexus*.

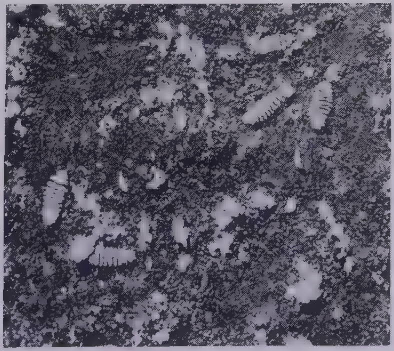


FIG. 5. Five mature larvae of *P. impexus* feeding on *Adelges*-infested tree. Photo. Dr. J. Franz.

disappear until none are to be seen towards the middle of the month (observations at Seegraeben, in 1950). Probably this gradual diminution of the numbers of adults begins when the daily temperature reaches 10°C. and is complete when the temperature drops below 5°C. The adults seek their hiding places when the nights become colder in October and remain in these winter quarters until the following spring.

Hibernation of the adults lasts about six months and usually takes place in the crevices of the bark near old knots on infested trees. *P. impexus* leaves its hibernation place in the first sunny days of spring (25th March 1951, at Seegraeben), and returns to hiding at any noticeable drop in temperature. It is usually permanently out of hiding by the time the first-instar larvae appear; this is generally during the first or second fortnight of April. Oviposition is resumed in April and in May. During the last period of its life the adult remains on the *Adelges* infestation, copulating frequently and preying on the Aphid population.

The activity of the adults in relation to that of the Aphid seems to be entirely conditioned by temperature. The adult becomes torpid when exposed to a temperature lower than 10–15°C. A drop in temperature in spring and autumn has a very marked effect and the adults remain motionless, and without feeding, on the infested trees. Activity begins again as soon as the temperature rises. The adults are most active against the *Adelges* population during their main oviposition period in autumn and in the three spring months. They show a very reduced activity between these two periods and remain dormant for about 6 months.

The most important period for the development of the population of the predator is the main oviposition period, which takes place during the autumn generation of *A. piceae*, but both the spring and the autumn seasons are equally important with respect to biological control. The scarcity of food in the month of July and part of August is probably responsible for some dispersal of the predator. Up to the present time no experiments have been conducted to investigate the importance of dispersion. Weise (1884) found *P. impexus* adults in July on *Picea excelsa* in Germany. The supposition of aestivation is not readily acceptable since some individuals are present all summer on the trees attacked by the Aphid. On the other hand it is thought possible that some of the *P. impexus* adults return to the *A. piceae* infestation about the middle of the summer, especially if we compare the number of individuals that remain on the trees in July with the number found later, in September.

A few observations seem to indicate that the adults, having once reached the infested tree, do not show any particular sensitiveness. They do not appear to be able to distinguish a heavily from a lightly infested tree, and their search for food appears to be a random one. Flying was observed very infrequently and consisted of flights of a few metres only.

Diet: *P. impexus* feeds on eggs and sistentes of every instar. Residues of food are found in the mid-gut (Pl. XX, fig. 1). Some dissections have shown the mesenteron to contain at times large numbers of fungal spores (Pl. XX, fig. 2), introduced perhaps with the usual food. It is not known whether any supplementary food is ingested by the predators.

It is difficult to estimate the quantity of food ingested by the adult. This is, of course, dependent upon the season, being greater in the two periods coinciding with spring and autumn generations of *Adelges*. The adults seldom feed when the weather is bad. The density of the Aphid population and that of the population of the other predators present (Diptera, Coleoptera, Neuroptera) on the infestation also has a marked influence on the food consumed. The adult *P. impexus* does not feed at night.

Some information on the voracity of the adults and therefore their value from the standpoint of biological control was collected. The larval activity in the third and fourth instars is considered aggressive, disorganising and rapid, whereas the adult activity is slow but continuous. The following data was assembled during the autumn infestation of *Adelges*.

—An adult feeding for a day at the end of July (24th–27th) consumed on the average 5·3 neosistentes;
—an adult destroyed in one day at the beginning of August (10th–12th) 5·75 neosistentes;
—an adult fed in one day (12th–13th August) on 11 neosistentes;
—in the course of 7 afternoon hours (14th–15th August) an adult fed on 6 neosistentes;
—in 17 hours (the night included) between 14th–15th August, an adult consumed on the average 8 neosistentes and 3 sistentes II;
—in 39 hours (two nights included) between 16th–18th August, an adult destroyed an average of 12 neosistentes and 3 sistentes II;
—in 4 hours (14th August) 5 adults destroyed 10 neosistentes, 70 sistentes II and one sistens IV with 19 eggs.

It is very difficult to express mathematically the average voracity of adults of *P. impexus*, owing to the varying behaviour of each individual in a given time. From the preceding and following data we may learn more about the behaviour of the adults than if we attempt to formulate any opinion concerning their average voracity. The sistentes III and IV are never completely consumed by *P. impexus* adults. The dead or slightly sucked Aphids may be greater in number than those totally devoured and this fact is of particular importance. Generally a waste of food is observed, chiefly when the *Adelges* population is dense.

—In 60 hours (26th–29th August) two adults devoured 7 sistentes III and 9 sistentes IV;
—in 59 hours (26th–29th August) an adult destroyed an average of 3·6 adult Aphids per day;
—in 74 hours (26th–29th August) two adults destroyed 6 sistentes II, 15 sistentes III, 13 sistentes IV with almost all the eggs of the broods;
—in 59 hours (27th–30th August) an adult consumed an average of 3·4 sistentes per day;
—in 48 hours (27th–29th August) two adults destroyed 33 eggs;
—in 50 hours (27th–29th August) two adults devoured 34 sistentes III and 31 sistentes IV with 65 eggs;
—in 48 hours (27th–29th August) three adults devoured 34 sistentes III, 27 sistentes IV with almost all the eggs of their broods;
—in 47 hours (29th–31st August) an adult destroyed an average of 8 Aphids per day;
—in 10 days (27th August–6th September) an adult destroyed 17 sistentes III and 47 sistentes IV with eggs in great numbers;
—in 72 hours at the end August two adults devoured 6 sistentes II, 15 sistentes III and 13 sistentes IV (without eggs);
—in 120 hours (1st–5th September) male and female together fed on 204 eggs;
—in 120 hours (1st–5th September) single adults destroyed an average of 17 sistentes IV with their broods;
—in 120 hours (1st–5th September) an adult fed upon 156 *Adelges* eggs.

The behaviour of one adult in a given time was observed. The adult was placed into a rearing tube with a sistens and its 18 eggs, at a temperature of 22°C. For eight minutes the adult was seen running up and down the tube, passing near the Aphid three times before finally settling at the eggs. Remaining in its normal position, it destroyed one egg after the other, until after the lapse of

6 minutes 21 seconds it attacked the sistens and fed upon it for a period of 6 min. 14 sec. The next egg was devoured during 1 min. 16 sec., it then searched for the other eggs and ate them in 10 min. 23 sec., after which it cleaned its tarsi and mouth parts for one minute. Again it fed on eggs for 2 min. 57 sec., cleaned its tarsi and mouth parts, fed, cleaned again and departed. Altogether the *P. impexus* adult took about 40 minutes to destroy an Aphid with 17 eggs, spending about a third of its time cleaning itself and searching for food. It failed to attack one egg only, perhaps because the feeding behaviour is connected with the touching of prey.

In relation to lack of food, an experiment was set up at the laboratory (at 20°C.) with material collected at Winterthur on 28th August, 1952. Among the adults of *P. impexus* left in the rearing tubes without *A. piceae* for food, mortality was observed on the fifth day of starvation and reached its maximum on the ninth day. The last of the adults died on 11th September. In an experiment performed in Munich beginning on 13th September with material collected at Laimbach, at a temperature varying between 12° and 20°C., Dr. J. Franz noted that mortality among the adults was lower and only 50 per cent. of the insects died in September. The last of the survivors died on 5th October.

Egg and oviposition period.

a. Time and place of oviposition.—Eggs are deposited in nature in protected places or are hidden in the residues of the wax secreted by the Aphids of the spring generation (Pl. XX, fig. 3), especially where the *Adelges* infestation has been intense as at Naenikon in 1950. They are also found in the moss partially covering the trunk of infested *A. alba*, in crevices of the bark and frequently in the crevices of the knots (the most favoured place), in the empty puparia of *Cremifania nigrocellulata* and of *Leucopomyia obscura*, in the pupal exuviae of *Aphidecta obliterata* and in the larval exuviae of *Laricobius erichsoni*. In only one instance was an egg of *P. impexus* found unprotected on the smooth bark.

The location of the eggs on the trees is random, depending upon the conformation of the hiding place and on the position required by the female for oviposition. The eggs may be deposited in a horizontal, vertical or an oblique position on the tree. Probably no fluid is secreted for fixing the egg to the substrate and perhaps the fluid substance covering the egg as it leaves the genital chamber is sufficient. The eggs are generally deposited singly. In the crevice of one knot four eggs were found, separated from one another and perhaps laid by different females. Two eggs close together and laid by the same female were seldom observed. According to Dr. Wichmann the deposition of an egg takes 3 to 4 minutes.

Generally, oviposition begins in August. At Spoeck (Bavaria), in 1950 a female of *P. impexus* was observed by Dr. Wichmann to lay the first egg on 21st July in a rearing tube. In Switzerland the first eggs were found in nature on 20th August 1950, at Seegraeben. The oviposition period extends to the first cool autumn days, generally until October, when the adults seek their winter quarters. The eggs do not hatch till the spring.

Oviposition is practically limited to the period mentioned above. After hibernation, however, the adults continue laying eggs on the infested trees in April and May, and freshly deposited eggs may be observed at the time when the first pupae of the new generation are to be seen (field and laboratory, 1952). Samples of these spring eggs never hatched during the next few months. They were kept in the laboratory from May till October, some at a constant temperature of 20°C., some at temperatures ranging from 20° to 7°C., and a beginning of embryonic development was to be observed in August. It is possible, therefore, that these eggs attain the same embryonic development in autumn as that of the autumnal eggs. Some spring eggs were noticed on the trees in September 1952. Although rare, they were easy to distinguish from the freshly deposited autumn ones.

In July 1951, when all the adults of the new generation had emerged, a third-instar larva was noticed on an infestation in Germany. According to Dr. Franz, the same thing happened in the previous year. Such an exceptional case suggests the possibility of an abnormal hatching of an autumnal egg rather than the hatching of an egg laid in the spring. Even if late egg-hatching (which very seldom happens) could be associated in nature with the spring oviposition, these isolated cases are of no importance from the biological control point of view. The larvae emerging from overwintered eggs provide the only successful action against the *Adelges* infestation.

b. Fecundity.—The results of ten experiments carried out simultaneously in the laboratory and lasting three days are given here. They were investigated at a constant temperature of 20°C. at the end of August 1952.

TABLE I.

Oviposition in captivity and degree of parasitism of adults of *P. impexus*.

Rearing tube no. ..	1	2	3	4	5	6	7	8	9	10
Adults per tube ..	19	19	19	18	19	18	20	20	19	20
Females per tube ..	12	4	8	6	10	10	10	11	5	8
No. of eggs laid (3 days)	37	19	23	38	32	42	19	45	16	16
Adults parasitised by *Centistes scymni* ..	2	3	6	3	—	3	7	3	8	10
Females parasitised by *Centistes scymni* ..	2	—	3	—	—	1	4	2	2	5
Laying females ..	10	4	5	6	10	9	6	9	3	3

Material collected at Winterthur, August 1952.

From this Table we infer that 65 females deposited 287 eggs in three days; an average of three eggs per female every other day. If it be considered that the autumn oviposition period lasts from two and a half months to three months, then a female will deposit from 80 to 100 eggs. It must be kept in mind that towards the end of the period (October) the weather is not as favourable as it is in August or September.

From the Table it is seen that account was taken only of the first three days of oviposition in captivity since the number of eggs deposited diminishes considerably in the subsequent days, and after the sixth day mortality among adult males and females was observed. In rearing tube no. 8 the number of the eggs fell from 45 to 4 in the second series of three days, and remained at 4 in the third series; in tube no. 6 the number of eggs fell from 42 to 9 and in the third series to 8.

c. Development of the eggs.—The embryonic development was studied in collaboration with Dr. G. Krause of Munich during the winter 1950–51, using material collected both in Switzerland and in Germany. In nature, during the winter, eggs of *P. impexus* go through a latent life stage during embryonic development from the moment when the abdominal extremity of the embryo reaches the dorsal mid-point of the egg to the moment when its abdomen shortens (so that its extremity reaches the posterior pole of the egg) and the eye pigmentation appears. The period of latency does not occupy a very definite period. It has been generally observed that this stage is reached in September, as was the case at Seegraeben in 1950, and such embryos may be found as late as in February. It is therefore possible that the eggs deposited in the period August–September develop rather rapidly until they reach a certain embryonic stage and in this condition they remain until the end of the winter.

The eggs kept in the laboratory (Munich) for the winter hatched in April and did not develop more rapidly than in the field. This suggests that room temperatures with very little fluctuation do not affect the length of the embryonic life. According to Dr. Franz, eggs left under natural winter conditions until 20th December at Laimbach, and then taken to room temperatures did develop faster, one specimen hatching in January as a normal larva. It is therefore possible for the embryo to develop from the moment it reaches its latent stage, and further development may be caused by a considerable change of temperature.

d. Vitality and mortality of the eggs.—*P. impexus* eggs collected at Seegraeben and on the Pfannenstiel (near Feldmeilen) were put on filter paper in petri-dishes covered with muslin (organdie) and kept at the meteorological station on the Pfannenstiel (850 m.) until 10th December. The temperature dropped to a minimum of −6°C. on 5th December. Thirty eggs were held for three consecutive weeks at −12°, −25°, −12°C., respectively, and thirty eggs for three weeks at −12°C. without interruption. They were then returned to natural winter conditions, where the temperature reached −8°C. only once at the end of February (1951). All the eggs held for three weeks at −12°C. hatched simultaneously on 21st April. Eighty per cent. of the eggs held at −25°C. hatched on 21st April, 15 per cent. hatched during the next three days and the mortality was 5 per cent. The eggs overwintered on the Pfannenstiel (winter minimum −9°C.) also hatched simultaneously on 21st April and a mortality of 3 per cent. was noted.

From these few experiments on the resistance to winter temperatures in Europe it seems probable that any eggs deposited in Canada would survive the extremes of weather to be encountered there.

It is difficult to evaluate the mortality of eggs deposited in nature, since they are present at the end of summer along with numerous larvae of *C. nigrocellulata*, *C. latitarsis*, *L. obscura*, *A. thompsoni*, *C. ventralis*, etc. All these predators probably destroy eggs of *P. impexus*. In addition there are mites living gregariously in the same overwintering places as the eggs and perhaps feeding upon them. Without the activity of the above-mentioned predators, it is thought that the egg mortality of *P. impexus*, from climatic extremes, would be very low or non-existent.

e. The egg and its hatching.—The egg (Pl. XX, fig. 3) is oval in shape, rather stocky and orange in colour. It measures 0·6–0·7 mm. in length and is twice as long as broad. The egg becomes lighter in colour at the end of the winter. At the end of its embryonic development it loses its gloss and just before hatching it is possible to see the segmentation of the mature embryo. At the right time the embryo breaks the chorion (by means of one of the egg-bursters) causing a short longitudinal split. Afterwards, the embryo presses its thorax against the opening and with longitudinal movements it succeeds in cutting the chorion with the next egg-burster. With movements of expansion and contraction and pressure against the chorion, the embryo extends the two slits and breaks the connection between. The hatching process lasts about 45 minutes.

In nature the time of hatching of overwintered eggs in any particular locality and year is fairly restricted. Nevertheless some variation of a few days exists due to the position of the tree in the infested zone and to the position of the egg on the tree. On the Pfannenstiel (near Feldmeilen) in 1950 the eggs hatched almost simultaneously between 1st and 3rd May and in the next year on 21st April. At Seegraeben they hatched in 1951 between 15th and 20th April, at Laimbach near Munich some days later. In 1952 egg-hatching took place at the beginning of April at Aathal and Winterthur$_1$ ("Försterhütte") and in the second half of the month at Winterthur$_2$ (fig. 3).

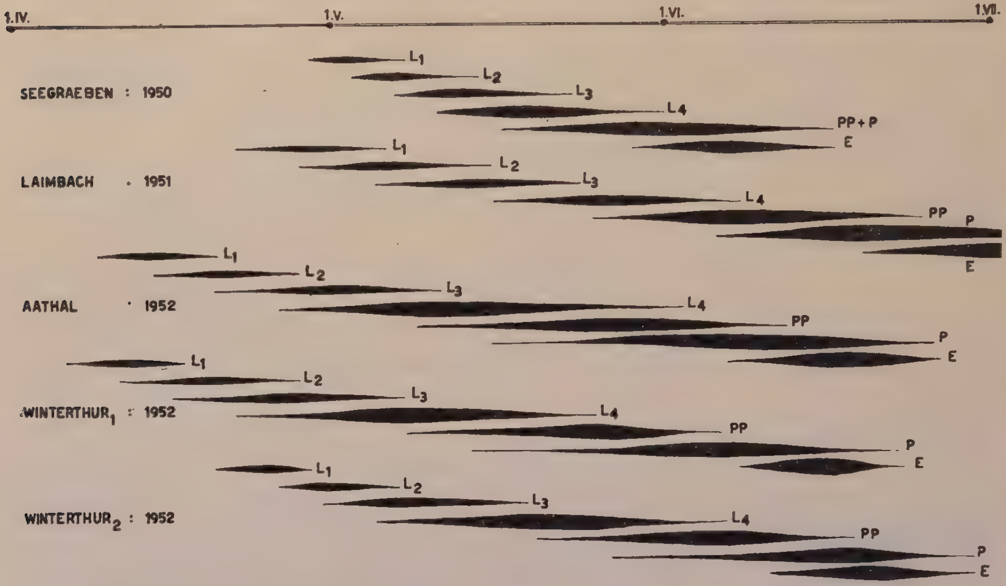


Fig. 3.—Development of the pre-imaginal instars of *P. impexus* in different localities and in different years.

Larval development.

a. The first-instar larva.—The newly hatched larva is orange with brown ocelli and brown egg-bursters and leaves the chorion without feeding on it. On the *Adelges*-infested trunks the newly hatched larvae are moving about near the old knots, near the crevices or on the moss, where the eggs had been deposited. At first they live more or less gregariously, then they disperse among the Aphid population. On the Pfannenstiel on 3rd May 1950, 130 larvae were gathered around the knots in a space of 80 cm. of trunk at 3 m. from the ground. First-instar larvae were found at Seegraeben from the end of April to 2nd–3rd May 1950 (fig. 3), having hatched after a cold period lasting for nearly all the second half of April. In 1952 at Aathal first-instar larvae were observed between 8th and 19th April, at Winterthur$_1$ between 5th and 14th April, and at Winterthur$_2$ between 19th and 28th April (fig. 3).

At a laboratory temperature of about 17°C. the first larval instar lasts five days.

Diet: The first-instar larva feeds on eggs and Aphids. The Aphids are attacked on their tergal region and the larva sinks its mouth parts into the wound. No haemolymph oozes from the wound since the predatory larva has such strong sucking power. The feeding activity of the larva is rather slow and requires from 5 to 10 minutes to suck an egg of *Adelges*. The larva sinks its mandibles into the chorion and slowly sucks the egg contents. Beneath the anterior fronto-clypeal region of the head the movements of the internal mouth parts may be observed. The egg is emptied slowly, flattens, then is generally filled and emptied over and over again with a dark violet-coloured liquid originating in the mesenteron. The chorion of the egg is not consumed. The mid-gut liquid injection occurs when feeding on the Aphids as well, but is less visible.

The first-instar larva seldom feeds upon eggs or Aphids isolated on the bark. It prefers to plunge its head into a little heap of eggs near an egg-laying sistens and destroys many eggs without changing position.

b. The second-instar larva.—In nature the second-instar larvae of *P. impexus* were observed at Seegraeben in the first 10 days of May 1950, in 1951 at the end of April and at Laimbach during the first half of May. In 1952 they were noted at Aathal and Winterthur$_1$ at the end of April and at Winterthur$_2$ at the end of April–beginning of May (fig. 3).

At a laboratory temperature of about 17°C. the second larval instar requires four days for completion.

The feeding activity of the second-instar larva is more rapid than in the preceding instar. A newly moulted larva devoured 19 eggs and 4 sistentes IV in an hour in the laboratory. A single egg can be sucked in 30–90 seconds. It was noted that in this larval stage injection of the mid-gut liquid into the prey is a continuous process and the reabsorption of the injected liquid which is an intermittent process appears related to slight larval body movements. The destruction of a sistens IV takes longer, about 3–5 minutes. The Aphid is attacked and sucked so that it appears to have only about half of its initial volume remaining. The mid-gut liquids are then injected and the Aphid is refilled. The liquid injection is so violent at times that the Aphid may have a volume larger than its initial one. A larva of *P. impexus* of this stage that was left four days on 10 cm^2. of densely infested bark, devoured practically everything, leaving behind very few eggs and Aphids.

c. The third-instar larva.—In the first half of May 1950 the third-instar larvae were observed at the same time in Seegraeben in Switzerland and at Spoek in Bavaria (observed by Dr. Wichmann). In 1951 they were seen at Seegraeben at the beginning of May and in Laimbach for two weeks in the same month. At Aathal and Winterthur$_1$ the larvae of this stage were present in the infestation at the end of April–beginning of May 1952, and at Winterthur$_2$ in the first fortnight of May (fig. 3).

The third larval stage lasts four days at the usual temperature of about 17°C.

The voracity and the mobility of these larvae on the tree increases considerably as compared with that of second instar. The larva III is able to destroy an egg in 20–50 seconds, and a sistens IV in 1–3 minutes. Its voracity was recorded as follows:

Larva III, two days after moult, observed in captivity during a given time at Laimbach near Munich at laboratory temperature 17° C.

In 30 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
75 seconds 1 *Adelges* egg destroyed, mid-gut liquid 4 times injected,
15 seconds food search,
45 seconds 1 *Adelges* egg destroyed, mid-gut liquid 3 times injected,
15 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
45 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
15 seconds food search,
90 seconds 1 *Adelges* egg destroyed, no injection,
15 seconds food search,
75 seconds 1 *Adelges* egg destroyed, no injection,
120 seconds food search,
120 seconds 1 *Adelges* egg destroyed, no injection,
30 seconds food search,
30 seconds 1 *Adelges* egg destroyed, no injection,
20 seconds food search,
70 seconds 1 *Adelges* egg destroyed, no injection,

10 seconds food search,
40 seconds 1 *Adelges* egg destroyed, no injection,
20 seconds food search,
50 seconds 1 *Adelges* egg destroyed, once injected,
150 seconds food search,
60 seconds 1 *Adelges* egg destroyed, mid-gut liquid twice injected,
120 seconds 1 *Adelges* egg destroyed, no injection,
60 seconds food search,
60 seconds 1 egg punctured, slightly sucked and then left. It contained an Aphid embryo.

The *P. impexus* larva destroyed 15 *Adelges* eggs in a rearing tube in 23 minutes. The eggs belonged to two broods only. After eating the 15th egg, roving began on the bark without any further egg destruction.

The following test with a larva starved for two hours indicates larval voracity:

Larva observed for two hours, laboratory temperature 25° C.

Larva feeds on 1 egg; 39 sec. — searches for food; 11 sec.;
,, ,, ,, 1 egg; 54 sec. — ,, ,, ,, 32 sec.;
,, ,, ,, 1 Aphid; 2 min. 7 sec. — ,, ,, ,, 21 sec.;
,, attacks a sistens but leaves it after 36 sec.;
rest time;
larva feeds on 1 Aphid; 3 min. 14 sec. — searches for food; 35 sec.;
,, ,, ,, 1 Aphid; 1 min. 2 sec. — ,, ,, ,, 4 sec.;
,, ,, ,, 1 Aphid; 29 sec. — ,, ,, ,, 2 sec.;
,, ,, ,, 1 Aphid; 25 sec. — ,, ,, ,, 12 sec.;
,, ,, ,, 1 egg; 1 min. 48 sec. — ,, ,, ,, 15 sec.;
,, ,, ,, 1 egg; 1 min. 15 sec. — ,, ,, ,, 21 sec.;
,, ,, ,, 1 egg; 50 sec. — ,, ,, ,, 6 sec.;
,, ,, ,, 1 egg; 54 sec. — ,, ,, ,, 5 sec.;
,, ,, ,, 1 Aphid; 1 min. 36 sec. — ,, ,, ,, 6 sec.;
,, ,, ,, 1 egg; 27 sec. — ,, ,, ,, 2 sec.;
,, ,, ,, 1 egg; 2 min. 4 sec. — ,, ,, ,, 3 sec.;
,, ,, ,, 1 egg; 1 min. 1 sec. —
rest time;
larva feeds on 1 egg 49 sec., egg not entirely devoured;
rest time;
larva feeds on 1 egg; 1 min. 15 sec. — searches for food; 3 sec.;
,, ,, ,, 1 Aphid; 1 min. 29 sec. — ,, ,, ,, 2 sec.;
,, ,, ,, 1 egg; 29 sec. — ,, ,, ,, 11 sec.;
,, ,, ,, 1 egg; 1 min. 17 sec. — ,, ,, ,, 3 sec.;
,, ,, ,, 1 Aphid; 7 min. 55 sec. — ,, ,, ,, 13 sec.;
,, ,, ,, 1 egg; 2 sec. (only punctured) searches for food; 36 sec.;
,, ,, ,, 1 egg; 1 min. 12 sec.
rest time;
larva feeds on 1 Aphid; 4 min. 6 sec. — searches for food; 7 sec.;
,, ,, ,, the same Aphid again; 9 sec.
rest time;
larva feeds on 1 egg; 7 sec., egg not entirely devoured;
rest time; searches for food 7 sec.; rest time;
larva feeds on 1 egg; 59 sec. — searches for food; 35 sec.;
,, ,, ,, 1 egg; 1 min. 16 sec. — ,, ,, ,, 1 min. 3 sec.;
,, ,, ,, 1 egg; 1 min. 12 sec. — ,, ,, ,, 24 sec.;
,, ,, ,, 1 egg; 47 sec. —

In two hours of observation the larva III fed upon 20 eggs and ten sistentes.

d. The mature larva.—Mature larvae (Pl. XX, figs. 4 & 5) have been observed at Seegraeben in 1950 during the last 20 days of May, in great number at Naenikon between 9th and 20th May where the density of fourth-instar larvae of *P. impexus* reached 25–30 individuals per dm^2., at Binz near Zurich until the beginning of June and at Kalberstein in Bavaria (observed by Dr. Wichmann) until 28th May. In 1951 mature larvae were found at Seegraeben from 6th May, at Laimbach from 15th May until the first ten days of June and at Berchtesgaden a little later. In 1952 at Aathal and Winterthur, larvae IV were present on the infestation from the end of April and during whole May, at Winterthur$_2$ during May until beginning of June (fig. 3).

At a laboratory temperature of about 17°C. the fourth larval stage lasts 17 days, the first half with normal larval activity on the *Adelges* infestation and the second half corresponding to the prepupal period. On the chart (fig. 3) this second period has been described separately since sufficient data were collected at Laimbach, Aathal and Winterthur.

The mature larvae are particularly voracious. They sink their heads into the *Adelges* broods with particular violence, break them up and destroy them. Sometimes the destruction of an egg does not require more than ten seconds and one larva destroys whole broods in rapid succession. These fourth-instar larvae seem to specialise in egg destruction rather than in killing Aphids. Considering the short developmental time of the larva IV, limited to 5–7 days, among the *Adelges* population, its efficiency is very great. The increase of the body volume of the larva in the first four days after the moult (fig. 4) is a good measure of estimating the larval voracity. Such an increase in size does not occur during other larval stages.

At Naenikon the Aphid population on 9th May 1950 entirely covered the trunk of *A. alba*, making them whitish. The population was almost completely destroyed in ten days time by a population of fourth-instar larvae of *P. impexus* estimated at 3,500–4,000 larvae for each infested tree. In this infested locality together with *P. impexus* there existed only a few specimens of other predatory species, such as *L. obscura*, *C. ventralis*, *L. erichsoni* and *A. thompsoni*. The

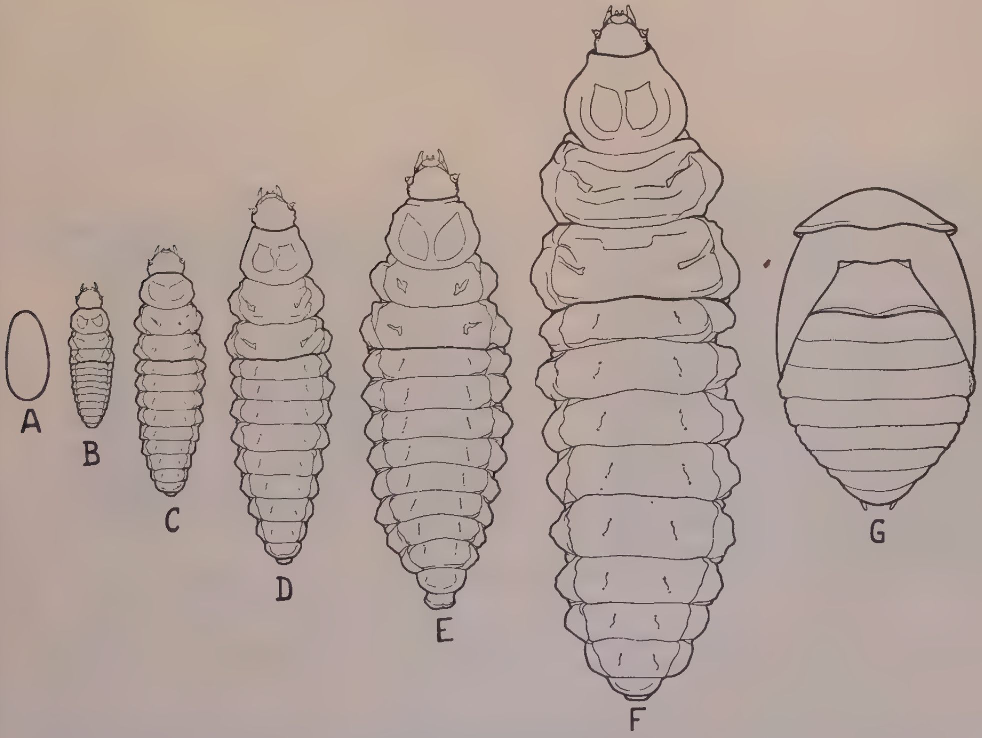


Fig. 4.—Increase of the body volume during the larval time: A, egg; B, first-instar larva after hatching; C, D, E, 2nd-, 3rd- and 4th-instar larva, respectively, after moult; F, four-day-old mature larva; G, pupa.

destruction of the *Adelges* population was effected for all practical purposes by the *impexus* larvae only.

It is a striking and conspicuous fact that mature larvae descend from the upper to the lower part of the infested tree a few days before the prepupal period is beginning. This behaviour was noticed at Aathal early in May 1952. Every day the *P. impexus* larvae were collected from the lower portion of the tree (about 3 m. of trunk) for rearing in cages, and every day, for many days, on the same portion of the tree mature larvae were found by tens and sometimes by hundreds. Beneath the moss covering the basal portion on an infested tree at Winterthur 700 pupae were collected on 6th June 1952. In the last ten days of May a concentration of mature larvae was noticed here on the lower part of the trees. The results of collecting of pupae has always been very poor on those portions of the trees situated above 3 m. from the ground.

e. General considerations on the larval stages.—The newly hatched larva of *P. impexus* measures a little more than 1 mm. and is light orange in colour. The mean maximum width of the head is 0·204 mm., varying between 0·189 and 0·216 mm. The larva is easy to recognise, having on its prothoracic plates the characteristic egg-bursters, strongly chitinised and standing out on the orange-coloured body. To separate the subsequent instars the head-capsules must be measured. The measurements were taken from a hundred individuals in each stage collected at different localities. The maximum head width for the second-instar larva averages 0·252 mm., varying between 0·229 and 0·270 mm.; for the third-instar larva it averages 0·309 mm., varying between 0·297 and 0·324 and for the mature larva has a value of 0·386 mm., varying between 0·364 and 0·405 mm. (fig. 5). The colour of the second-, third- and fourth-instar larva, as well as that of first-instar after a short period of feeding, is darker orange than the newly hatched one or those immediately after a moult.

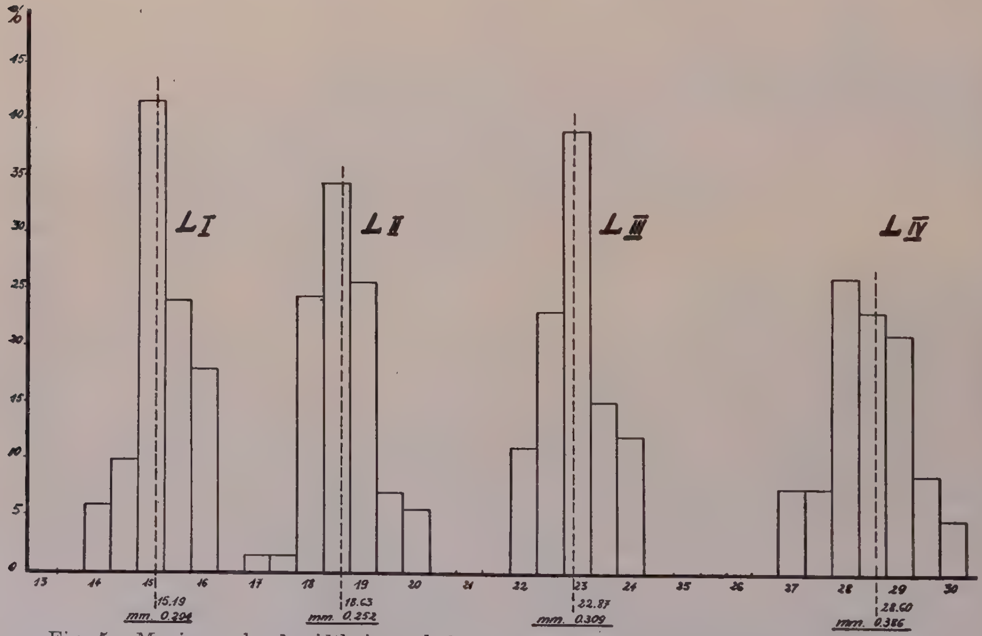


Fig. 5.—Maximum head width in each larval stage. The actual measurements of head width are shown in micrometer units, the mean for each instar being converted into mm.

The remarkable increase of the body volume from the first to the fourth

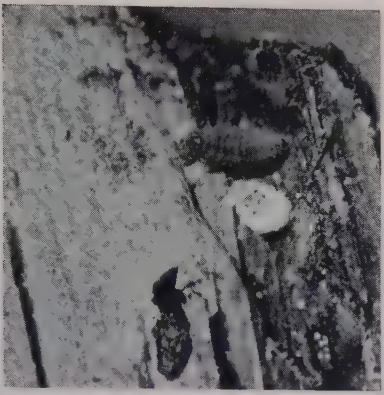


FIG. 1. Fourth-instar larva of *P. impexus* immediately after the moult.

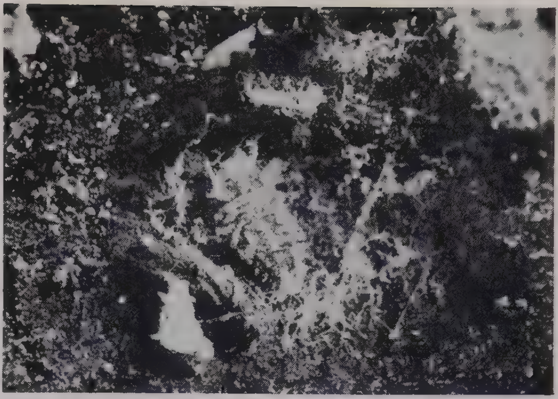


FIG. 2. A prepupa of *P. impexus* in the spun network on the bark.

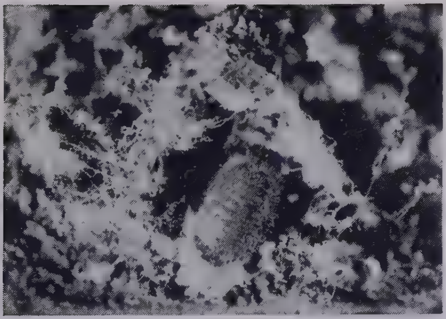


FIG. 3. A pupa of *P. impexus* in the spun network on infested bark.

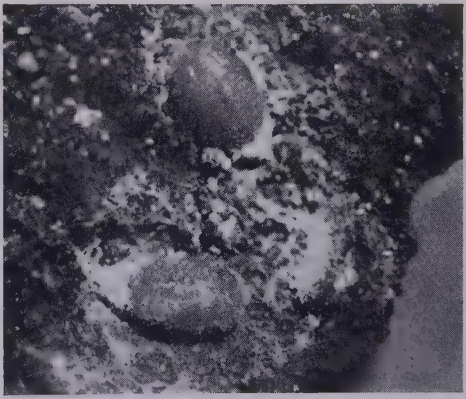


FIG. 4. Pupae of *P. impexus* on the bark without spun network.

instar is shown in fig. 4. This increase is particularly evident during the last instar from the moult to the prepupal period. The length-ratio between the head, thorax and abdomen of larva I is 6 : 15·5 : 19, of the mature larva after the moult 12 : 40 : 65 and of the four-day-old mature larva 12 : 67 : 105. The increase in body volume of the mature larva during the first four days is more or less equal to the increase in the first three stages combined. The importance of the larva IV is therefore evident from the biological control standpoint. The thoracic and almost the whole of the abdominal cavity are occupied by the mid-gut only. The four-day-old mature larva measures about 5 mm. in length, after the third moult 3·2 mm., the early third-instar larva after the second moult measures 2·5 mm. and the second-instar larva after the first moult measures 1·75 mm.

The exuviae of larvae of *P. impexus* are not generally found among the Adelgid population since moulting (Pl. XXI, fig. 1) usually takes place in protected bark areas (old knots). In the laboratory rearing tubes the larvae moult beneath the bark or in a dark corner. The moulting process is rapid and the wax secretion starts at once.

Prepupa and pupa.

The pupal stage begins after a prepupal period of 8 to 9 days. In previously described hiding places on the bark surface (see p. 262) the fourth-instar larva spins a kind of " cocoon " composed of silk filaments (Pl. XXI, figs. 2, 3). The mature larva in the laboratory rearing tube moves to the darkest corner and the spun network composing the " cocoon " has no definite arrangement. The base of the network in contact with the bark consists of intertwined vertical and horizontal filaments joining the floor of the hiding place to the overhead covering. In this irregular cocoon network may be found residual *Adelges* wax, wax of the larva left from the spinning process, dead crawlers and residues of sistentes IV and of eggs, etc. The threads are fixed to the substrate with a brown-coloured secretion. The network looks closely woven and probably is an aid in preventing the entrance of predators. When the overhead covering of the hiding place is removed the whole network collapses (Pl. XXI, fig. 3). The filaments extend farther than the immediate surroundings of the prepupa, indicating that the spinning movements are irregular and therefore do not fit any set pattern. Not every mature larva spins this network (Pl. XXI, fig. 4). During the prepupal period the mature larva gets considerably shorter, looks withered (Pl. XXI, fig. 2) and the wax covering all the tergites appears disorderly. The moult then begins and the next stage lasts about ten days at a laboratory temperature of 20°C.

The larval stages of *P. impexus* are synchronised with the *Adelges* population, especially the fourth-instar larva which seems to be closely related to the most active time in the *Adelges* population development. The pupal period on the other hand is present during the decline of the host population.

Pupae were found at Seegraeben in 1950 from 15th May onwards, at Naenikon from 20th May onwards, and at Winterthur on 2nd June. In 1951, at Seegraeben the first pupae were collected in the first fortnight of May, at Laimbach near Munich at the beginning of June only, at Tussenhausen (Bavaria) on 17th June. At Aathal and Winterthur$_1$ the first pupae were noted on 14th–15th May 1952, and at Winterthur$_2$ a little later (fig. 3).

General considerations of the life cycle of P. impexus *in Switzerland and in Germany.*

From the observations described above it is concluded that *P. impexus* has only one generation a year. The complete cycle from the hatching of the egg to the emergence of the adult takes about six weeks. Eggs deposited on the infested trees in the late summer and the beginning of the autumn produce larvae in April after a slow embryonic development during the winter. The hatching of the larvae coincides with the start of the *Adelges* infestation and the larval development coincides with the most active time of the spring generation of the Aphid. *Thus the mature larvae achieve the greatest value from the viewpoint of biological control.* The imagines, on the contrary, although they are present from spring to autumn have a *slow but persistent* influence and do not succeed in changing the degree of infestation of the autumn generation.

Factors limiting the Development of the Population of *P. impexus*.

In addition to the influence of the host, *A. piceae*, on the development of the population of *P. impexus* there are other factors of environmental resistance in the form of parasites. These parasites are the two new species, *Scymnophagus mesnili* and *Centistes scymni*, described below. *C. scymni* is by far the more effective, parasitising an average of from 25 to 30 per cent. of the females of the new generation (22·8 per cent. at Winterthur (see Table I); 32 per cent. at Aathal). This results in the loss of a third or even a half of the *P. impexus* larvae, which would otherwise be present on the infested trees the next spring. *S. mesnili* attacks a rather small percentage of pupae and therefore has no great influence on the numerical status of the Coccinellid population.

Scymnophagus mesnili.

S. mesnili is a new species of the palearctic region, the specific name for which was proposed by Dr. Ch. Ferrière in 1950, and he has kindly allowed his original description of the species to be published in this paper.

a. Description by Dr. Ch. Ferrière.

" *Scymnophagus mesnili*, n.sp. (PTEROMALIDAE, PTEROMALINAE):

" Female: body dark bluish-green, the scutellum more aeneous, the abdomen " shining green at the base and along the sides. Antennae brown, scape and " flagellum below yellowish. Legs with the coxae greenish-brown, the femora " light brown, the tibiae and tarsi yellow, with very faint brownish lines on " middle and hind tibiae. Head finely shagreened, narrowed behind the eyes; " ocelli forming a very low triangle, the lateral ocelli not much farther distant " from each other than from the eye-margins; eyes short oval; temples very " narrow in the middle; cheeks straight, converging towards the mouth; front " margin of clypeus excavated in the middle; both mandibles with four teeth. " Antennae inserted in middle of the face, short; scape reaching to the level of " the front ocellus, pedicel longer than broad, three anelli very small, the five " funicle joints subquadrate, subequal in length and in breadth, club three-" jointed, not broader than the funicle and about as long as three preceding " joints together. Thorax very finely reticulate, the reticulation a little broader " on the mesonotum than on the scutellum; parapsidal furrows very short; " scutellum with a narrow transverse furrow; propodeum without median carina, " but with a rounded nucha, which is more strongly punctate than the rest of " the propodeum. Wings hyaline; marginal vein somewhat thickened, shorter " than the postmarginal vein and about as long as the narrow stigmal vein. " Legs relatively short and narrow. Abdomen about as long and as broad as " the thorax, the first visible tergite as long as the third of the abdomen; " ovipositor scarcely protruding. Length 1·2 mm.

" Male unknown.

" Type deposited at the British Museum (Natural History), London; several " females have been obtained at the laboratory of Prof. L. P. Mesnil, to whom " I have the pleasure to dedicate this species.

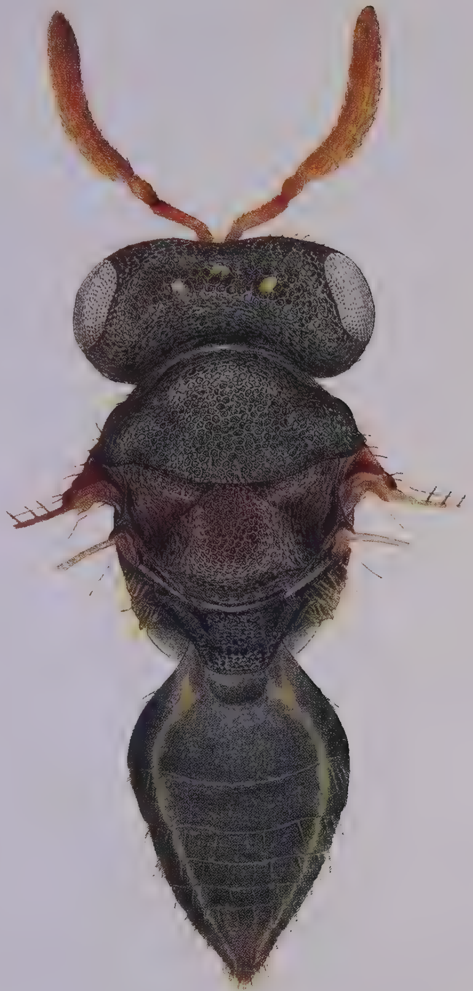


FIG. 1. *Scymnophagus mesnili*, sp.n., dorsal view.

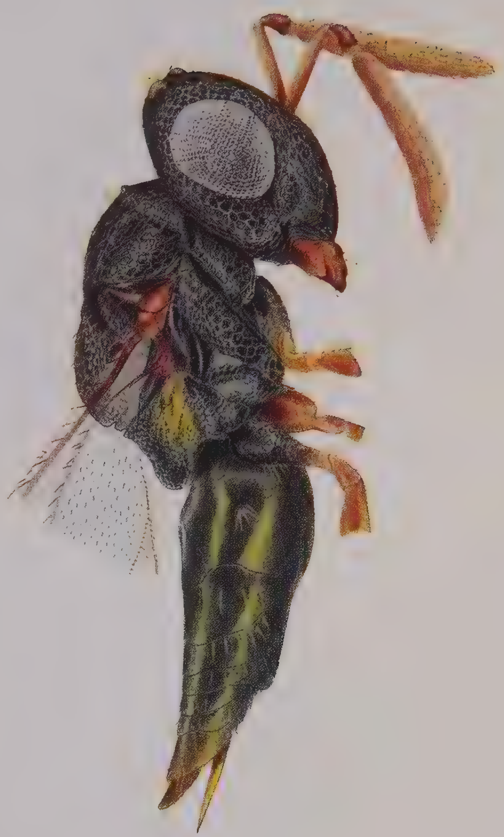


FIG. 2. *Scymnophagus mesnili*, sp.n., lateral view.

"This is the first representative of the genus in Europe, but it is very "closely related to the North American species *S. townsendi* Ashm. Mr. A. B. "Gahan kindly sent us specimens of this species from the United States and "from Japan, which were obtained from Scymnid pupae. Compared with our "European species, they can be distinguished as follows:

"*S. townsendi*: body black, scarcely dark bluish on the face only, greenish "at the base of the abdomen; abdomen and legs more yellow; head larger, "distinctly broader than the thorax; abdomen narrower than the thorax, more "pointed behind; propodeum as strongly punctate at base as on the nucha;

"*S. mesnili*: body dark green; antennae and legs more brownish, the coxae "more or less dark metallic green; head scarcely broader and abdomen not "narrower than the thorax; propodeum with punctation smaller at the base "than on the nucha.

"The specimens from Japan are similar to the American species in the black "body and the relative size of head, thorax and abdomen, but have darker "coxae. Another species, *S. secundus* Crawford 1912 (*Proc. U.S. nat. Mus.*, "**43,** p. 172) was obtained in East Africa, Uganda, from a *Scymnus* sp. or allied "genus; specimens of that species from Kenya, bred from the Coccinellid "*Hyperaspis senegalensis* (Muls.) are in the British Museum. This species is "also much similar to *S. townsendi*, but differs, according to Crawford, by the "more distinctly differentiated furrow on the scutellum and the less distinct "sculpture of the propodeum laterad of the lateral folds.' A fourth species, "*Xenocrepis mexicana* Girault 1916 (*Ent. News*, **27,** p. 223), parasite of a "Coccinellid predator of *Saissetia oleae* (Bern.) in Mexico is probably also a "*Scymnophagus*.

"The genera *Scymnophagus* Ashm. and *Xenocrepis* Foerst. are very closely "related and very similar in the more or less broadened marginal vein and the "short antennae with three anelli and five funicle joints. They cannot be "synonymised however since they differ mainly by the form of the propodeum, "which in *Scymnophagus* has a distinct punctate nucha and no median carina, "whereas in *Xenocrepis* there is no nucha but a distinct median carina and well "marked lateral folds.

"*Xenocrepis* Foerst. is a valid genus the type of which, based on Foerster's "specimens, should be *X. pura* Mayr. It was a confusion of names which "induced Ashmead to synonymise *Xenocrepis* Foerst. and *Caenocrepis* Ths., "two quite different genera. *Xenocrepis pura* Mayr has five funicle joints and "is a real PTEROMALINAE, whereas *Caenocrepis arenicola* Ths. has six funicle "joints and belongs to the METASTENINAE, with two spurs on the hind tibiae."

b. Source of the material.—The first adults of *S. mesnili* (Pl. XXII, figs. 1, 2; text fig. 6) emerged in the laboratory at Feldmeilen from pupae of *P. impexus* collected at Seegraeben between 16th and 25th June 1950. In Germany Dr. J. Franz observed adult emergence between 28th June and 7th July in Spoeck (Bavaria). In the spring of 1951, at the German substation of our laboratory (Munich) some examples emerged from pupae of *P. impexus* which had remained, because of parasitism, in the pupal stage from the preceding spring. The parasite was also observed in 1951, in two Bavarian localities (Tussenhausen and Laimbach) infested with *A. piceae*. In the Swiss localities Naenikon, Pfannenstiel and Winterthur the Coccinellid pupae were found free from parasites.

c. Life history of S. mesnili.—The life history of this Pteromalid is not yet completely known. From parasitised pupae of *P. impexus* collected in June 1950 at Seegraeben all the parasites emerged in the laboratory within ten days (Pl. XXIII, figs. 1, 2). From parasitised pupae collected at Spoeck (Bavaria) on 6th June of the same year, the emergence of the parasites was *partial* and a number of *Scymnophagus* remained in larval diapause until the next spring, *i.e.* for a period of ten months. It is not yet known what happens to the parasites which emerge in June and July without having gone through a diapause period. Possibly a secondary host in which *S. mesnili* is able to develop further generations exists. This would allow the parasites to emerge the next spring.

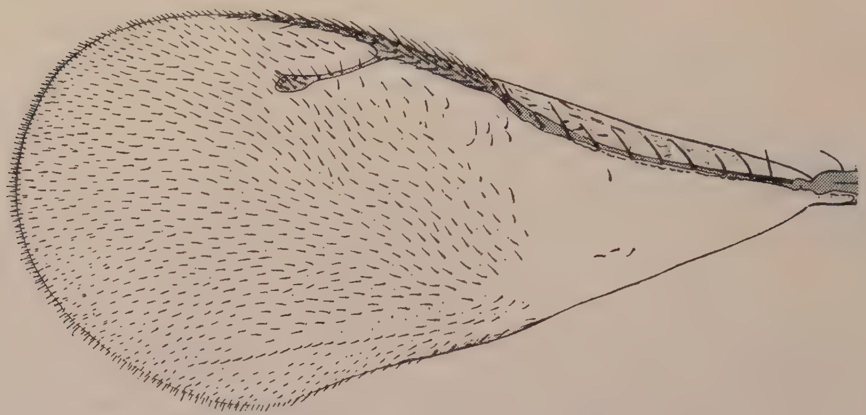


Fig. 6.—Left fore wing of *S. mesnili*.

Scymnophagus has not emerged from any other predators of *A. piceae* in the laboratory and the diagram of the life history as shown in fig. 7 corresponds to the data at present available. The parasite attacks the pupae of *P. impexus*.

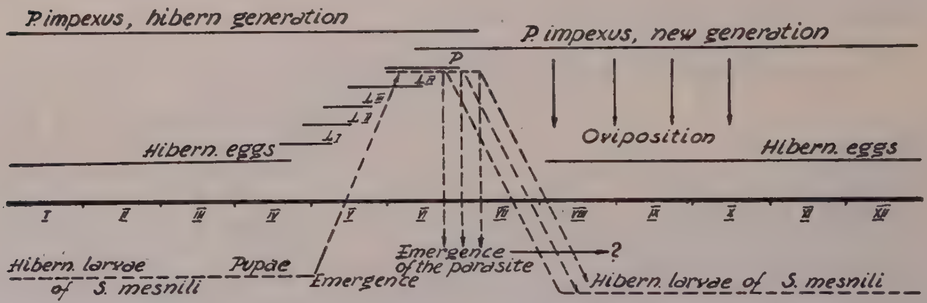

P. impexus, hibern generation
P. impexus, new generation
P
L I
L II
L III
L IV
Hibern. eggs
Oviposition
Hibern. eggs
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
Hibern. larvae of S. mesnili
Pupae
Emergence
Emergence of the parasite
?
Hibern. larvae of S. mesnili

Fig. 7.—Life history of *S. mesnili* in relation to that of *P. impexus*.

The degree of parasitism by *S. mesnili* was not very high in the past few years. Out of 1,000 pupae of *P. impexus* collected at Tussenhausen (Bavaria) on 17th June 1951, 126 were parasitised; out of 1,124 pupae collected at Laimbach, near Munich, in the first days of June, 61 (5·4 per cent.) contained parasites; out of 1,200 pupae collected at Aathal (Switzerland) in May 1952, only ten proved to be parasitised.

The parasitised pupae of *P. impexus* are easy to distinguish by their light brown colour, which differs from the reddish brown of the healthy ones. Each Coccinellid pupa usually contains two individuals of *S. mesnili* lying face to face (Pl. XXIII, fig. 1) in their pupal stage. The parasitised pupae are to be found in the spots where *P. impexus* normally spends its pupal period.

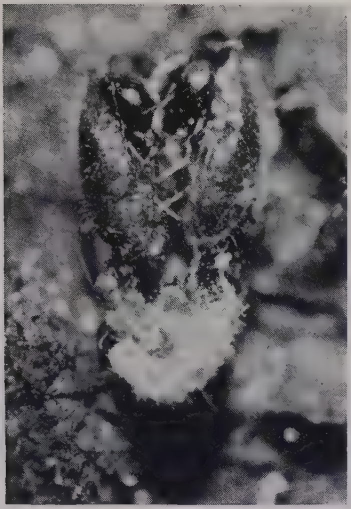


FIG. 1. Two pupae of *S. mesnili* in a pupa of *P. impexus*; Seegraeben, June 1950.

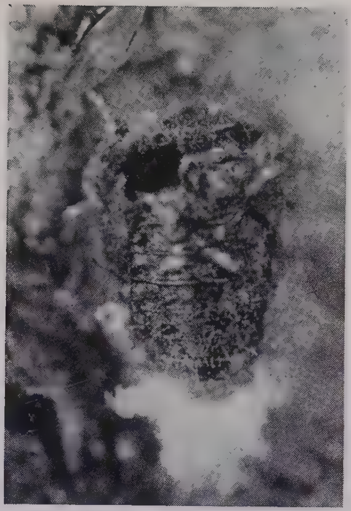


FIG. 2. Hole in the thorax of a pupa of *P. impexus* after the emergence of the parasites (*S. mesnili*); Seegraeben, July 1950.

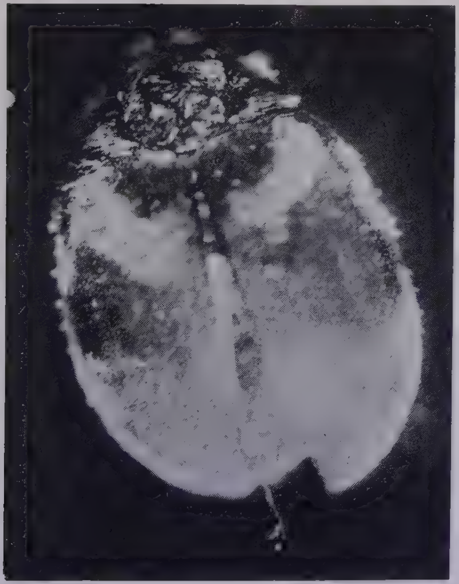


FIG. 3. Normal appearance of adult of *P. impexus* after emergence of larva of *C. scymni*.

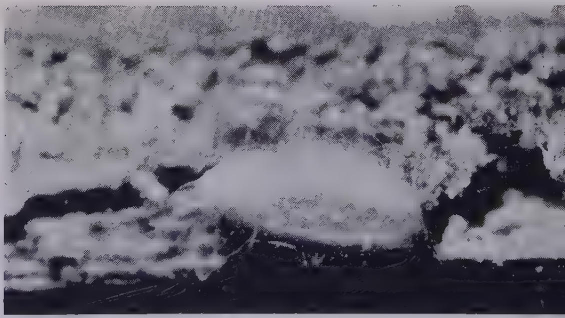


FIG. 4. Cocoon of *S. scymni* on the infested bark of *Abies alba*.

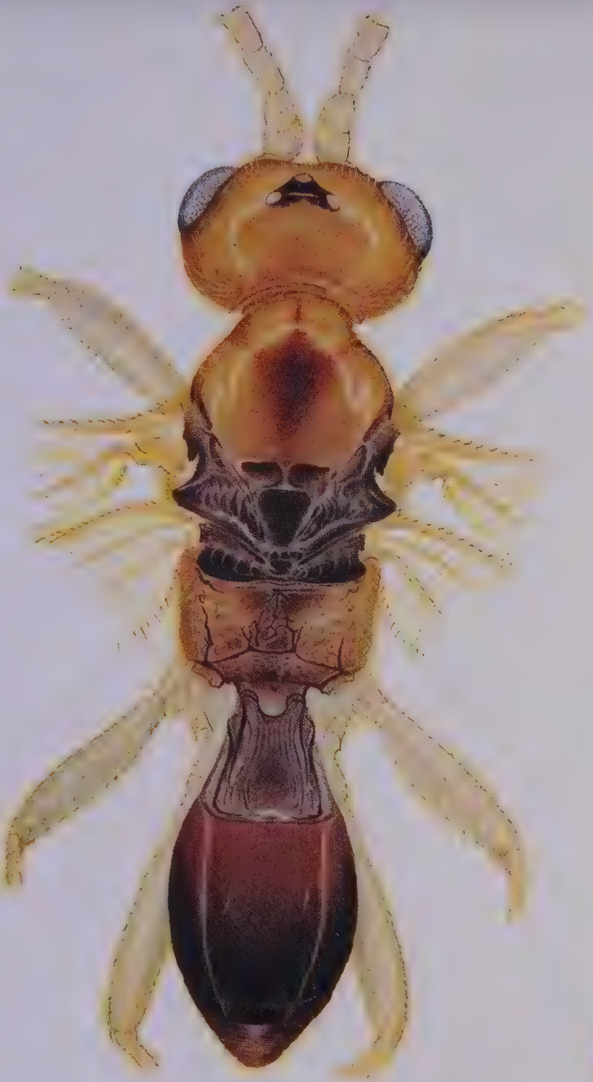


FIG. 1. *Centistes scymni*, sp.n., dorsal view.

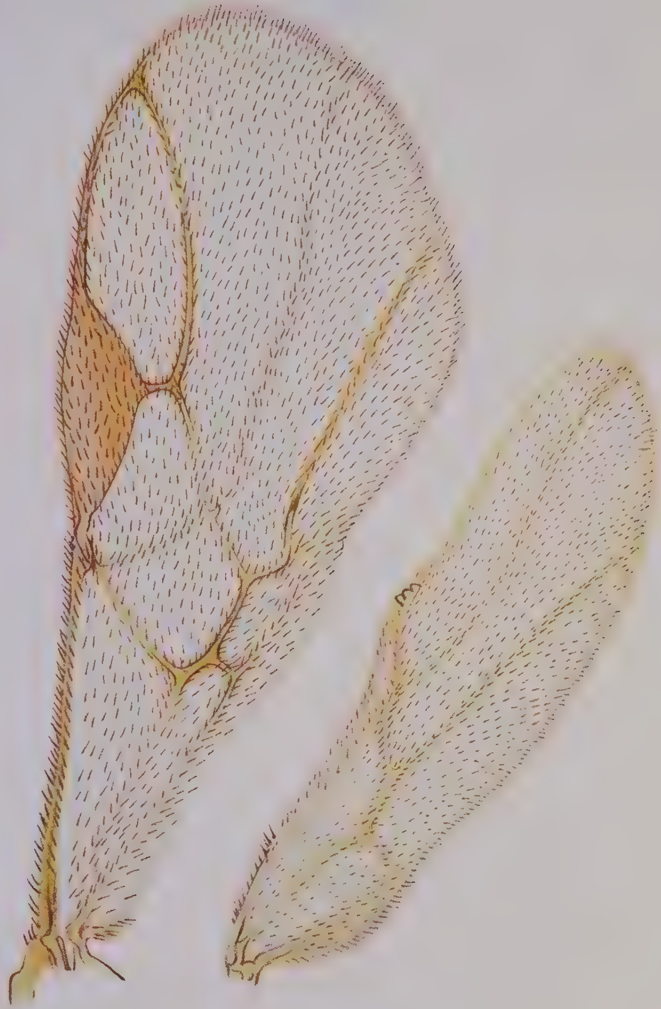


FIG. 2. *Centistes scymni*, sp.n., anterior and posterior wings.

Centistes scymni.

The original description of this species, drawn up by Dr. Ch. Ferrière, is, with his permission, included below.

a. Description by Dr. Ch. Ferrière.

"*Centistes scymni*, n.sp. (BRACONIDAE, LEIOPHRONINAE):

"Female: head orange-yellow, only the stemmaticum blackish; the clypeus "and mandibles lighter yellow. Thorax and abdomen black, the propleurae, "mesopleurae and metapleurae reddish, as are also the first abdominal segment "and the sides of the second. Antennae brown, the three first joints yellow. "Legs entirely yellow, coxae included. Stigma and veins in the wings brown.

"Head smooth, narrowed behind the eyes, ocelli forming a small regular "triangle, the lateral ocelli twice closer to each other than to the eye-margin; "seen from in front, the head is rounded, the vertex arched, the cheeks short; "clypeus well separated from the face; mandibles with the upper tooth longer "and more pointed than the lower tooth. Antennae with 22 joints, almost as "long as the body, inserted in the middle of the face, the points of insertion "more distant from each other than from the eyes; first joint short, about twice "as long as broad, the second rounded, the third a little longer than the first, "the following joints all longer than broad, but gradually shorter and narrower. "Thorax smooth, only the propodeum more or less finely rugulose; mesonotum "without parapsidal furrows; scutellum small; propodeum with a distinct arched "transversal carina in the middle, the supero-median area faintly marked. "Wings large, as long as the body, the stigma broad, triangular, the first "abscissa of the radial vein very short, about three times shorter than the "breadth of the stigma, the second abscissa curved, the radial cell closed; two "cubital cells, the first separated from the discoidal by a distinct vein; recurrent "vein interstitial, shorter than the transverse-cubital vein; anulus postfurcal; "parallel vein inserted near the base of the brachial cell, where this cell is open; "nervellus not broken. Legs relatively strong, with short ciliae. Abdomen "shorter and narrower than the thorax, the first segment a little longer than "broad, finely striate, the following segments smooth, slightly compressed from "the sides. Ovipositor curved like a scythe and directed under the abdomen "towards the thorax, reaching beyond the middle of the abdomen. Length "2 mm.

"Male unknown.

"Type deposited at the British Museum (Natural History), London.

"Although some LEIOPHRONINAE have been described from different parts of "the world, the members of this subfamily are still rare and not well known. "Only two species of *Centistes* had been found in Europe, both described by "Nees. *C. fuscipes* Nees is distinguished by its short antennae with 19 joints, "its short ovipositor, as long as the fourth of the abdomen and its brown legs; "*C. lucidator* Nees, more common, has long antennae with 24 joints, ovipositor "as long as the first segment, and is entirely shining black with only mandibles "and clypeus testaceous; *C. scymni* is easily distinguished by its entirely yellow "head, reddish sides of the thorax, antennae with 22 joints and longer ovipositor, "which is longer than half the length of the abdomen.

"Nothing is known about the biology of the two older species. In De "Gaulle's catalogue, *C. fuscipes* is given as the parasite of an *Elachista*, "probably by error. The LEIOPHRONINAE are all probably parasites of small "Coleoptera as are *C. scymni* and the few *Leiophron* spp. of which the hosts "are known."

b. Source of the material.—This parasite (Pl. XXIV, figs. 1, 2) was found in five localities: at Seegraeben (Switzerland) and Spoeck (Bavaria) in 1950, at Laimbach (Bavaria) in 1951 and at Aathal and Winterthur (Switzerland) in 1952. In other localities checked by this laboratory the parasite was not found in the three-year period. Mature larvae issued on 15th May 1950 and on 16th and 17th May 1952 from adults of *P. impexus* placed in rearing tubes at the Feldmeilen laboratory. From the resultant cocoons adults of *C. scymni* emerged at the end of May, and on 1st and 2nd June, respectively (temp. 20°C.).

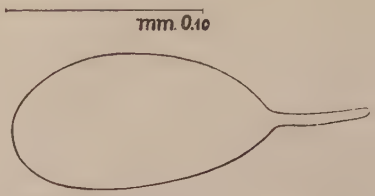


Fig. 8.—Egg of *C. scymni.*

c. Life history of the parasite.—*C. scymni* was present in 1950 on the *Adelges* infestations in June; it attacks *P. impexus* adults of the new generation. The parasite generally emerges from its cocoon after the appearance of the first new adults of *P. impexus* (laboratory checks). It attacks the host from the side, thrusting an egg (fig. 8) through the pleura into the abdomen. The eggs deposited in adults confined in rearing tubes were always arranged along the sides of the abdomen extending from the thorax to the genital opening. The stalk is always turned inwards. In the rearing tubes adults of *P. impexus* were found containing 3–5 parasite eggs in their abdominal cavities. Only one of them develops into a normal larva. The embryonic development takes place in June and July and the first-instar larva hibernates in the thoracic-abdominal cavity. The larva resumes development at the beginning of the spring and on maturing leaves the host through a hole cut between the 5th and 6th abdominal tergites (Pl. XXIII, fig. 3). Emergence is usually near the middle of May (observations at Seegraeben in 1950 and at Aathal in 1952). The mature larva issuing from the host measures about 3 mm. in length, is rose coloured and very active. It spins a white silken cocoon 2–2·5 mm. long (Pl. XXIII, fig. 4) and after a two-week pupal period (laboratory temperature of 20°C.) the adult emerges and attacks *P. impexus* of the new generation (fig. 9).

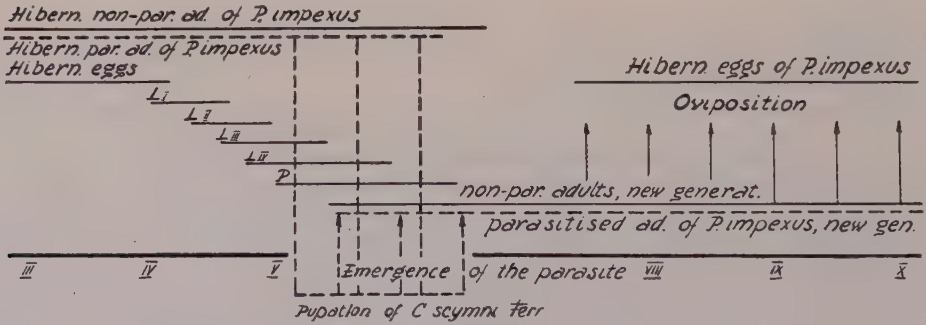
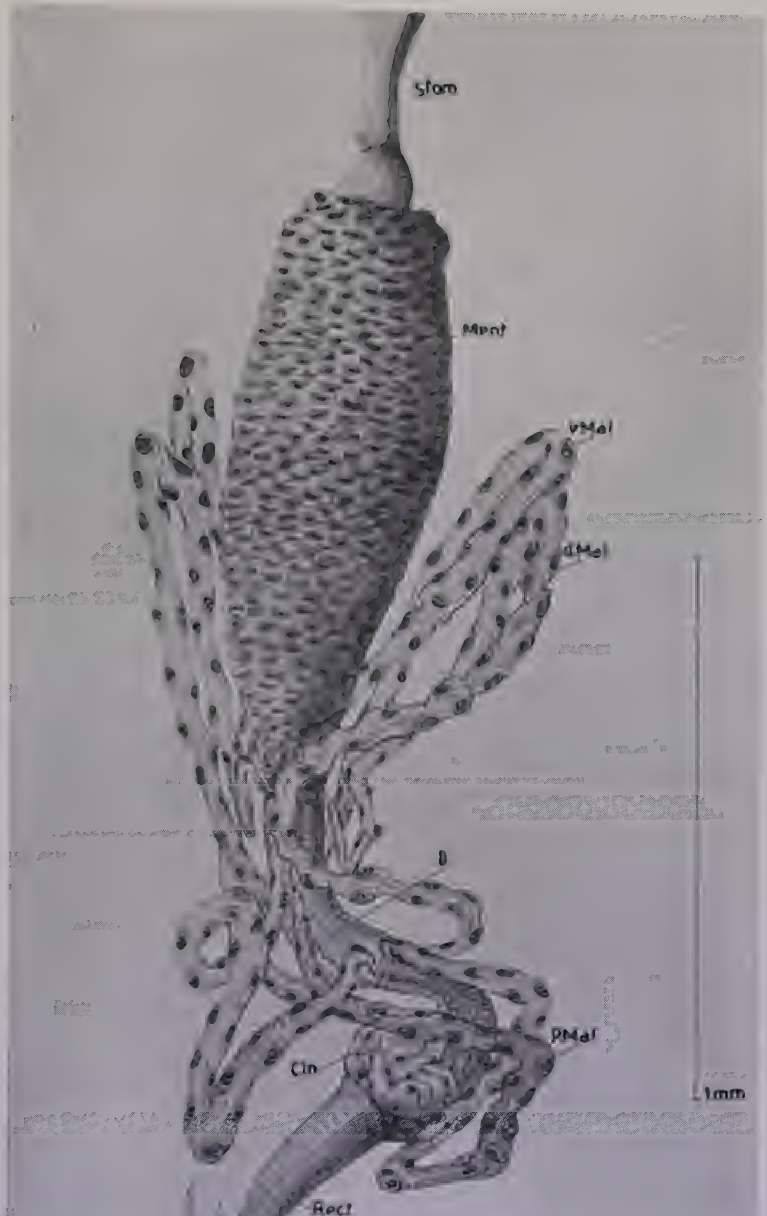

Hibern. non-par. ad. of P. impexus
Hibern. par. ad. of P. impexus
Hibern. eggs
L I
L II
L III
L IV
P
non-par. adults, new generat.
Hibern. eggs of P. impexus
Oviposition
parasitised ad. of P. impexus, new gen.
III
IV
V
Emergence
of the parasite
VIII
IX
X
Pupation of C. scymni ferr

Fig. 9.—Life history of *C. scymni* in relation to that of *P. impexus.*

d. Effect of the parasite and reaction of the host.—The growth of the parasite in the body of the host causes at first a strong inhibition of the development of the reproductive organs both in the male and in the female. From the practical point of view the parasite action on the male is of no significance. On the other hand the effect it has on the female of *P. impexus* is important, inasmuch as the inhibition of ovarian development (fig. 10) prevents oviposition during the


Stom
Ment
vMal
dMal
PMal
Cln
Rect
An
1mm

Digestive tract of *P. impexus* adult: *Stom*, stomodaeum; *Ment*, mesenteron; *Il*, ileum; *Cln*, colon; *Rect*, rectum; *An*, anus; *d-*, *v-*, *pMal*, dorsal, ventral and posterior Malpighian tubes.

summer and the beginning of autumn. In the spring, the hibernated first-instar larva continues its growth and matures in a 6- to 8-week period. At this time it slowly consumes all the abdominal contents except the sclerotised parts. The parasitised adults of *P. impexus* live normally until the parasite larva emerges. The host reaction to the inhibition of ovarian development is marked by an abnormal production of adipose tissue which eventually fills the abdominal cavity.

The degree of parasitism by *C. scymni* is difficult to estimate, since a large

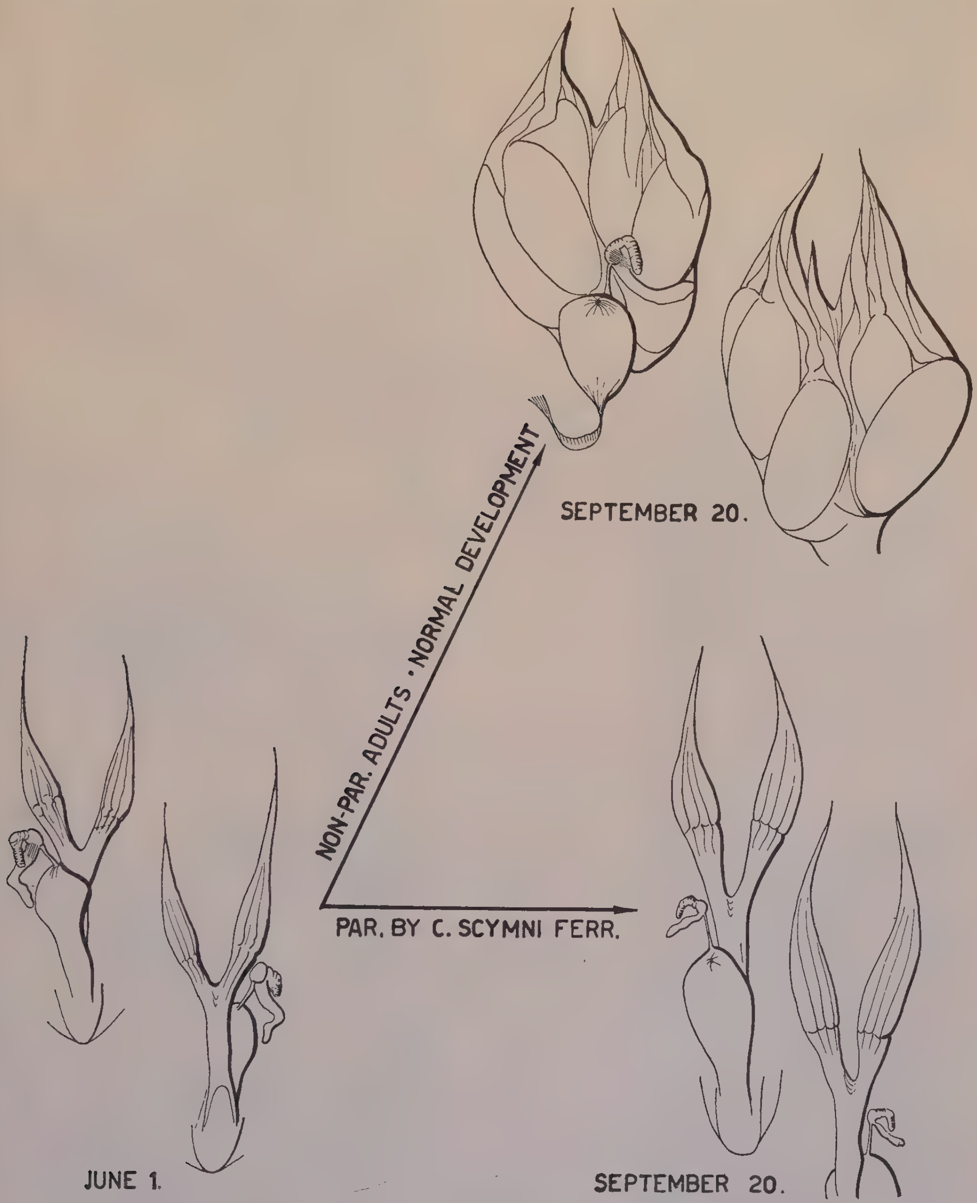

NON-PAR. ADULTS · NORMAL DEVELOPMENT
SEPTEMBER 20.
PAR. BY C. SCYMNI FERR.
JUNE 1.
SEPTEMBER 20.

Fig. 10.—Inhibition of ovarian development caused by *C. scymni*, compared with the normal development of ovaries in non-parasitised adults of *P. impexus*.

sample of adults of *P. impexus* should be taken in the autumn and in the spring. This is practically impossible for the adults are never observed in great number on the infestations of *A. piceae*. At the end of August 1952 it was possible to collect 191 adults of *P. impexus* at Winterthur. Forty-five of these were parasitised (23·5 per cent.). Of 130 adults of *P. impexus* collected at Aathal on 5th September 1952, 38·5 per cent. were parasitised. In both localities it was noticed that the degree of parasitism was higher in the males of *P. impexus* than in the females, with the result that 64 per cent. of the adults parasitised were males at Aathal, as were 58 per cent. of the parasitised adults at Winterthur (see Table I). At Seegraeben, the percentage parasitism in September 1950 amounted to 30 per cent., whereas in the preceding spring (from 6th to 13th May) 67 per cent. of the adults collected were parasitised. The percentage parasitism in spring appears high compared with that among insects collected in the autumn, possibly because non-parasitised adults die before or during the cold winter period. In the rearings a slight mortality occurred in September after the sixth day of captivity, but among the dead insects there were none which had been parasitised. On the other hand, the fat reserve with which the parasitised adults of *Pullus* are provided before hibernation might be the necessary requirement for survival.

Gregarines.

a. Source of the material.—In the mesenteron of both sexes of *P. impexus* (Pl. XXV) collected from spring to autumn in 1950 at Seegraeben and in 1951 at Laimbach, some Sporozoa belonging to the Gregarinida, group Cephalina (Steinhaus, 1947, 1949) were found. The body consisted of two compartments, the smaller being the protomerite and the larger the deutomerite which contains the nucleus. These cephaline gregarines were never found in larvae of *P. impexus* and are supposedly specific for the adults.

b. Notes on the life history and morphology of the known stages.—Though many dissections of mesenteron were made from adults collected during the whole year, it was possible to find only the stages composing the first part of the gregarine's normal cycle, that is from the sporozoite to the sporont. The remaining portion of the cycle is unknown and it is not yet possible to advance any satisfactory hypothesis.

The sporozoites (Pl. XXVI, figs. 1, 2) are to be found in the mesenteron of individuals in oviposition. They are mixed with gregarines of older stages corresponding probably to the sporonts. The sporozoites are elongate in shape, slightly arched, and consisting of a posterior more or less oval part and of a small conical anterior one. The dimensions are about 4–5 μ × 1 μ. The sporozoite fixes itself on an epithelial cell and grows at its expense. On the host cell the sporozoite develops into a trophozoite (Pl. XXVI, figs. 3, 4), which attains the dimensions of about 20–23 μ × 7–8 μ. The deutomerite of the trophozoite is rather stocky, more or less cylindrical in shape and its nucleus is evident. The trophozoite remains attached to the host cell by an organelle of attachment called the epimerite. In cross-section it is crescentic in shape and shorter but broader than the protomerite. At the proper developmental time the trophozoite leaves the epithelial cell of the host and becomes a sporont (Pl. XXVI, figs. 5, 6). The sporonts move about in the lumen of the mid-gut. They are pear shaped or rounded, with maximum dimensions of 0·15 mm. The gregarines in this stage fill the mid-gut of *P. impexus* in autumn, although some of the forms previously described may be present. The sporonts are still present in the spring (Pl. XXVI, fig. 5) in hibernated adults. The deutomerite contains a large nucleus (Pl. XXVII, fig. 2) in this stage. The nucleus is smaller than the protomerite, the cytoplasm is granular (Pl. XXVII, figs. 1, 2) and the epicyte

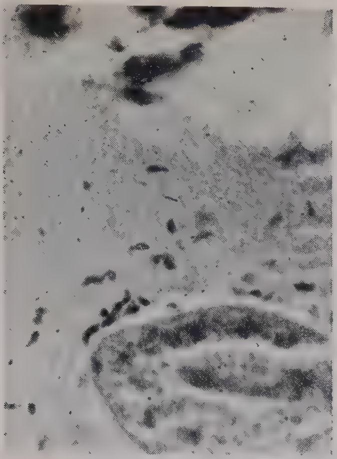


FIG. 1. Sporozoites free in the lumen of the mid-gut.

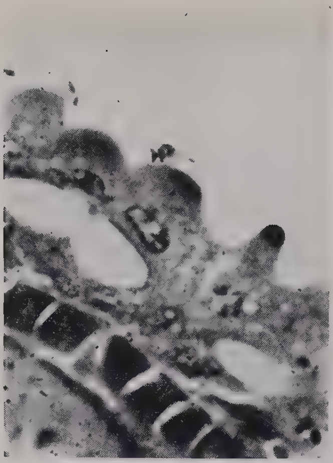


FIG. 2. Sporozoites fixed on an epithelial cell.

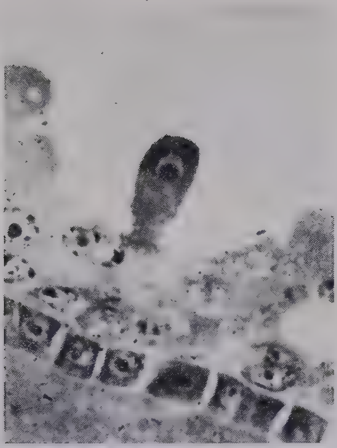


FIG. 3. Trophozoite attached to a cell near the nucleus.

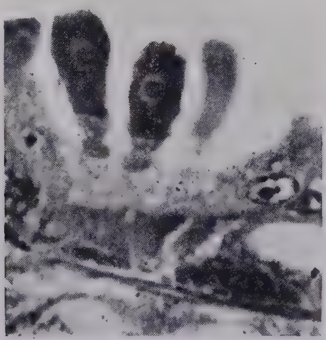


FIG. 4. More than one trophozoite attached to the same epithelial cell.

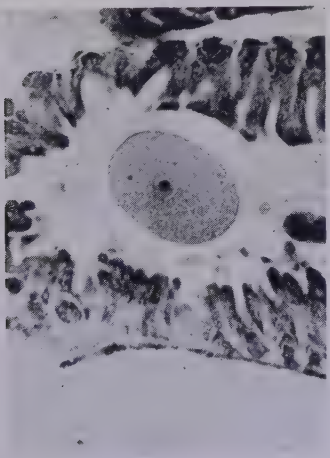


FIG. 5. Sporont in mid-gut of adult collected in the spring.

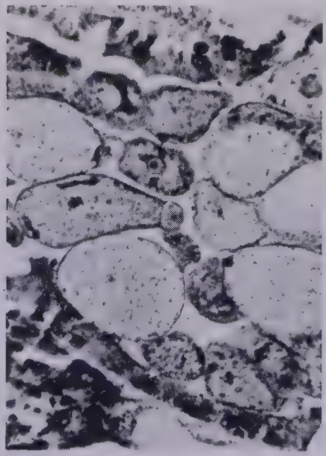


FIG. 6. Sporonts fill the mesenteron cavity of *P. impexus* adult collected in the autumn.

GREGARINES FROM MESENTERON OF *P. IMPEXUS*.

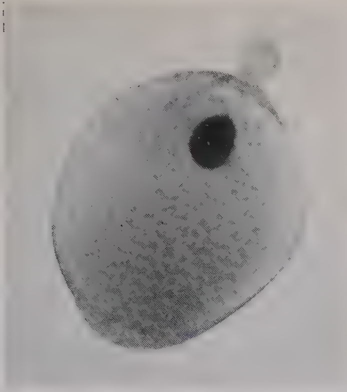


FIG. 1. Sporont rounded in shape, showing the granular cytoplasm and the relative sizes of protomerite, deutomerite and nucleus.

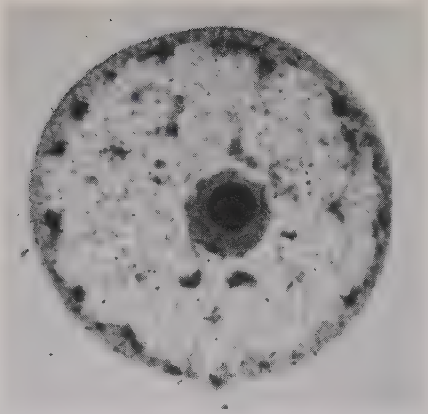


FIG. 2. Cross-section of a sporont showing the granular cytoplasm and the thinly furrowed epicyte.

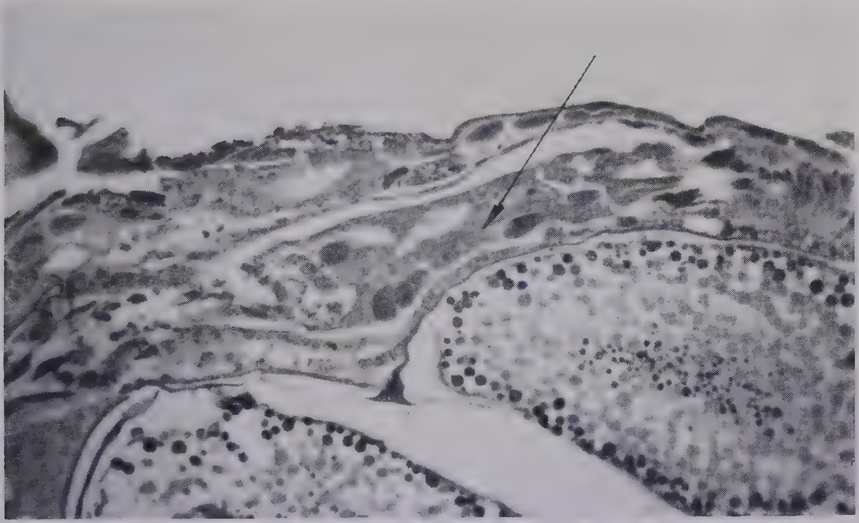


FIG. 3. Sporonts passing through the ileum of an adult of *P. impexus*.

GREGARINES FROM MESENTERON OF *P. IMPEXUS*.

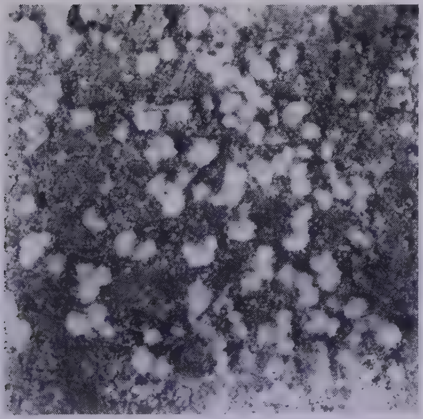


FIG. 4. Autumn infestation of *A. piceae* at Seegraeben 29th August 1950, after the action of predators in presence of their parasites and diseases.

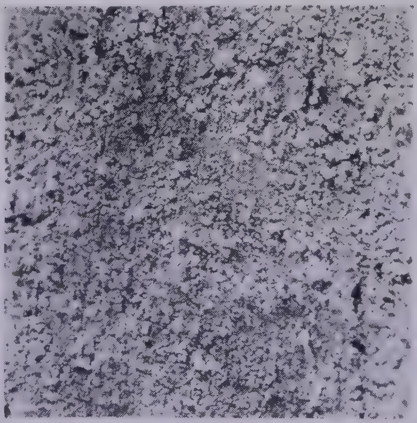


FIG. 5. Light autumn infestation at Naenikon, at the same time, after the action of a population of *P. impexus* almost free from other predators and parasites.

ACTIVITY OF PREDATORS IN TWO DIFFERENT LOCALITIES.

(Pl. XXVII, fig. 2) is very thinly furrowed. The natural colour of the gregarines is whitish.

The succeeding stages of the life cycle are not known. Forms identical with the sporonts contained in the mid-gut have frequently been observed in the ileum (Pl. XXVII, fig. 3) and rectum. These, however, had probably been evacuated from the mid-gut because of the large number present there.

c. Effect on the host and number of gregarines.—The gregarines are looked upon as parasites inasmuch as they are able to derive their nourishment from the host's organs. Their parasitic life begins with the trophozoite attached to the epithelial cell through its epimerite. The trophozoite increases its body volume considerably. The epithelial cell seems to be disintegrated by the effect of the trophozoite. The sporonts floating freely in the lumen of the mid-gut no doubt derive a considerable quantity of nutrient material through absorption. The increase in their body volume during this stage is evident.

The relationship of the gregarines to their hosts is not yet known. From the standpoint of biological control it would be important to establish whether the presence of gregarines reduces the ability of the adults of *P. impexus* to deposit eggs before winter.

The number of gregarines in the mid-gut of adults of *P. impexus* varies from season to season. Sporozoites in large numbers are found in late summer, a few months after the beginning of the new generation, but in this period of sporozoite formation it is possible to see a great number of forms of the two subsequent stages and often the sporonts fill the lumen. In the spring we generally find a few gregarines round in shape with a diameter of approximately 0·15 mm.

Nematodes.

A roundworm was found in the body of an adult collected at Seegraeben on 8th October 1950. This was the only example found during the period of the study. According to Dr. Menzel, of Wadenswil, the worm might belong to either of the genera *Mermis* or *Hexamermis*. It is difficult to determine because it is sexually immature. This is probably the first instance on record of Coccinellids being parasitised by Mermithids.

The worm, dissected from the body of a female of *P. impexus*, filled the abdomen and partially filled the thoracic cavity. It was wound around the digestive tract three times, with one end in a Malpighian tubule. The ileum of the host was longer than under normal conditions and the mesenteron more flattened. There was no trace of ovaries; however, the genital chamber and sclerotised parts of the genitalia remained.

This parasitism by a nematode has no importance, since only a single case has been observed. It could presumably assume a different aspect in biological control if the degree of parasitism should increase and so limit to some extent the oviposition of *P. impexus.*

Predators of P. impexus.

When there is a scarcity of the normal food, the predators of *Adelges* may easily prey upon one another. At Naenikon, in May 1950, some larvae of *Chrysopa ventralis* were observed destroying mature larvae of *P. impexus*; at Winterthur, on 2nd June 1950, mature larvae of *Cnemodon latitarsis* were seen feeding on pupae of *P. impexus* hidden in crevices of the bark; at Aathal, in May 1952, a mature larva of *Syrphus arcuatus* was sucking a larva IV of *P. impexus* and the numerous larvae of this Syrphid decimated the larvae and the prepupae in the rearing cages.

These occurrences are not frequent in nature and happen only when the *Adelges* population has been strongly reduced by the predators or when the population of a predacious species (as in the case of *P. impexus* at Naenikon) becomes very numerous and therefore undergoes the action of other predators. Predators of predators are generally the largest ones such as *Chrysopa*, *Syrphus*, *Cnemodon* and *Aphidecta*. In Germany, Dr. Franz observed the habits of the bird *Certhia familiaris* L. which in a quarter of an hour filled its bill three times with predatory larvae, particularly of *P. impexus*.

Estimate of the Controlling Value of *P. impexus*.

It is difficult to estimate the predatory activity of the single species *P. impexus* in its relations to *A. piceae*. It is even more difficult to express its value in relation to that of other predatory species living together with it.

The evaluation of *P. impexus* was not established on the basis of statistical data, from field experiments, but rather on facts observed in nature during the years 1950 to 1952. As to this Coccinellid, the localities from which the largest quantity of interesting observations were made were Seegraeben/Aathal and Naenikon.

At Seegraeben/Aathal, the site of an old *Adelges* infestation with many trees damaged in 1934, it was possible to find the greatest complex of control factors on *A. piceae*. Predator species and parasites and diseases of predators were all present. In this locality the *Adelges* infestation was present every spring and autumn, although the intensity was variable. Here the fluctuations of the number of each insect species were never extreme, but were always present and readily visible. At Seegraeben/Aathal we observed the action of every parasite species and disease, and the way it prevented excessive multiplication of the predator population. This often resulted in a more or less heavy *Adelges* infestation (Pl. XXVII, fig. 4). It is impossible to express the value of *P. impexus* at Seegraeben/Aathal, because it is difficult to separate or orient the the action of any one predatory species.

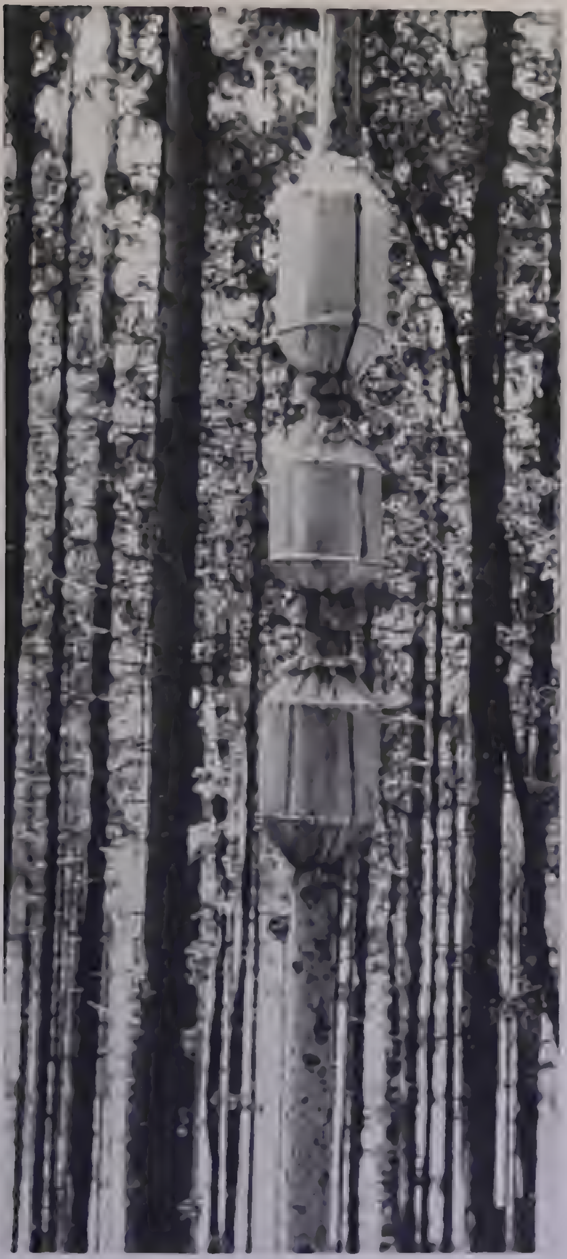
At Naenikon, a relatively newly established infestation was located on the border of the woods. In May 1950 the trunks of *A. alba* were completely covered with white *Adelges* wax. At this time a very heavy population of *P. impexus*, estimated at 25/30 larvae per dm². existed in close relation to some predatory species which were weakly represented numerically. It is believed that the population of *P. impexus* had reached, in relation to that of the *Adelges*, its highest point, for during the three or four week larval period it destroyed the Aphid infestation almost completely. At Naenikon neither *S. mesnili* nor *C. scymni* were found in numbers capable of reducing the predator action. Naenikon is one of the most important and rare instances showing the value of a predatory species. With the mass multiplication of the prey we observed the mass increase in number of the predator and with the mass destruction of the prey we found the predators almost completely dispersed (Pl. XXVII, fig. 5).

From the observations at Naenikon, where no important parasites limited the mass increase of *P. impexus*, it may be concluded that it would be advisable *to introduce this predator without its parasites to Canadian conditions.*

Rearing *P. impexus* and Shipment to Canada.

General plan of the work.

From the preliminary study carried out by this Laboratory in 1950, it was possible to plan the mass-rearing and shipping of *P. impexus* adults to Canada without their parasites. The importance of preliminary research as the basis of every biological control problem is evident. It is particularly important to screen and remove parasites and any disease organisms which might cause heavy mortality among the beneficial insects. During the mass-rearing in 1951, these



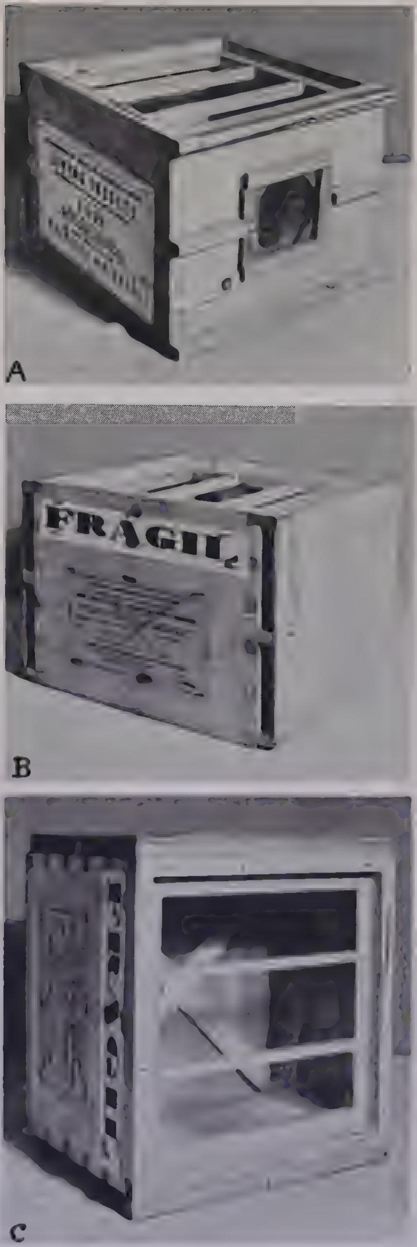


FIG. 1. Method of cage-rearing of *P. impexus* on infested trees.

Photo. Dr. J. Franz.

FIG. 2. Case used to ship *P. impexus* and other predators of *A. piceae* to Canada.

A, B, C. Different aspects of the case to show its special construction.

facts were not emphasised sufficiently and it is possible that the gregarines were introduced to Canada. In the mass-rearing technique three points require special attention:

a. To avoid the presence of *Scymnophagus mesnili* in the pupae of *P. impexus*, no shipping should be made of pupae collected in nature;

b. To avoid the presence of *Centistes scymni*, a very dangerous adult parasite, no shipping should be made of adults collected in nature;

c. To avoid any shipment of *P. impexus* adults containing gregarines, no shipment of individuals fed with *Adelges*-infested bark should be made.

The mass-rearing work was undertaken in 1951 in Germany with Dr. Franz, and in 1952 in Switzerland with the following instructions by Prof. L. P. Mesnil:

a. Building of cages in the infested forest of Laimbach (1951) and Aathal (1952) around the infested trees. The cages to be large enough to confine a considerable number of larvae of *P. impexus* of different instars, preferably of the fourth. These larvae should be collected in the immediate vicinity.

b. Removing the pupae from the rearing cages and separating the parasitised ones from the unparasitised ones.

c. Collecting pupae in other localities and separating as above.

d. Rearing pupae of *P. impexus* at the Laboratory to prevent parasitism by *C. scymni.*

e. Feeding newly emerged adults with nutritive solution until a sufficient number are accumulated to be sent to Canada. The danger of gregarines is thus avoided.

f. Shipment by air mail in special boxes.

Rearing cage.

The rearing cages in the field were built around the infested trunks to reduce the amount of work. No time was lost in feeding of larvae in cages. The cages prevented any activity by the parasite *S. mesnili* and assembled the pupae in one place so that the adults could be collected at the right time.

The cages (Pl. XXVIII, fig. 1) were raised from the ground 4–5 m. and fastened to the trunks so that they would not be disturbed. They are made of muslin (organdie) held away from the trunk by means of an upper and lower iron ring with four bars driven horizontally into the bark at equal distance from one another. Above and below the two iron rings the muslin is fitted to the tree. The muslin is provided with a zip fastener allowing free access to the cage. The muslin is brown in colour (1951) and blended well with the background. A black cloth was fastened around the trunk in the lower portion of the cage. This offered a convenient place for pupation. The cage was designed together with Dr. Franz. In 1952 the black cloth strip was replaced by a strip of corrugated cardboard held to the trunk with iron wire.

From 500 to 800 larvae of *P. impexus* were introduced into each cage in 1951. Of 3,050 larvae put in the cage at Laimbach between 13th and 26th May 1951, 80 per cent. were removed in the pupal stage between 11th and 16th June. The pupae were then taken to Munich and reared in tubes until the adults emerged. Between 17th and 23rd June 1951, more than 1,000 pupae were collected at Laimbach and 1,000 pupae at Tussenhausen. The adults which emerged were fed with agar-honey-sugar solution (Parker, 1948) and supplemented with *Adelges*, thus they may have contained Gregarines. The 4,050 adults were sent by air mail to Belleville (Dominion Parasite Laboratory) in special boxes containing from 500 to 850 individuals each.

In 1952 the number of larvae of *P. impexus* for each cage was increased to 800–1,000. From 11,000 larvae (see *, Table II) collected between 28th April and 6th May at Aathal, Horgen and Winterthur, and put into cages, 42 per cent. were destroyed by *Syrphus arcuatus* larvae present on the *A. piceae* infestations of eastern Switzerland. Unknowingly while the cages were being built on the trees, *S. arcuatus* eggs were enclosed and larvae penetrated under the corrugated cardboard. In some cages the predacious action of the *Syrphus* was so heavy that 90 per cent. of the *P. impexus* were destroyed. The cages were taken from the trees between 3rd and 11th June, when it was noticed that some Coccinellids were emerging and at the same time pupae were collected at Horgen, Aathal and Winterthur (Table II).

TABLE II.

Mass-rearing of *P. impexus* in Switzerland in 1952.

Locality	Larvae collected	Pupae collected	Adults emerged	Mortality of pupae in rearing tubes, incl. parasitism	% of mortality of pupae, incl. parasitism
Horgen	700	700	600	100	14·30
Aathal .. (wood) ..	9800 } 11000*	1200	700	500	41·70
Aathal .. (cages) ..		6350	6300	50	0·78
Winterthur ..	500	4200	4000	200	4·76
Total ..		12450	11600	850	Mean 6·83

The pupae collected in nature, or taken from the cages, were reared in tubes at a temperature of 20°C. until emergence. Each tube contained 500 pupae in a moist air current of 80 per cent. R.H. for the whole period. The 11,600 adults were shipped directly to Belleville without supplementary feeding, between 9th and 18th June, in boxes containing up to 1,300 adults each.

The high pupal mortality recorded in the last column of the Table is due to improper handling during collection. The mortality was highest at Aathal, since the collecting began there.

Shipping box.

The box employed for shipments of the predator is a slight modification of the one already used by this Laboratory in 1949 to send parasites to Australia. In the shipments of *P. impexus* to Canada in the spring of 1951, employing the new boxes, the mortality was 6 per cent.; in 1952 the mortality of *P. impexus* in the boxes sent to Canada was only 0·6 per cent.

The box (Pl. XXVIII, fig. 2) is built in such a way that it needs no particular care during shipment other than a temperature check. It is 24·5 × 24·5 × 20 cm. Two opposite walls have a hole in the centre 7–8 cm. in diameter which is covered on the inside with muslin (organdie), and on the outside with a brass-wire screen. The screen is further protected by a thin board of the same dimensions as the wall of the box itself. This board is fixed to battens so that it is 1·5 cm. from the net and permits air circulation. The board is also supplied with holes opposite the hole covered with the net. After adding these two boards the length of the box measures 28 cm. The interior of the box is provided, on the top, with a frame 1·5 cm. below the cover (cover not shown in Pl. XXVIII), to which a rather thick cellophane sheet is glued. This frame is held by four reinforcers at the corners. The cellophane is left in water for half an hour, then dried and applied directly to the frame. It permits customs inspection. Approximately 4 cm. from the bottom there is a wooden structure consisting of two small crossed boards fixed to the corner reinforcers. A square of organdie is glued to them. The space between the organdie and the box bottom is filled with moist sterilised sphagnum to maintain a constant relative humidity above 90 per cent. The organdie prevents the smallest insects from entering the sphagnum.

For the shipment of insects the inside of the box was provided, in 1951, with a wet sponge, wrapped in filter paper and fixed vertically at one corner of the box. This sponge was not included in the boxes in 1952. For food, the solution of Parker (1948) in drops on cardboard was placed on the inside of the box.

Before any insects were shipped to Canada, laboratory experiments were undertaken to determine their behaviour and survival in all stages and under varying conditions within the shipping boxes. Each insect species reacted differently and the mortality varied even for different stages of the same species. For the most part, the investigations were carried out at a temperature of 15°C. The relative humidity was varied, using sphagnum moss with different moisture contents and the insects were also tested both with and without the presence of artificial food.

Summary.

The biology of *Pullus impexus* (Muls.), a Coccinellid beetle predacious on *Adelges piceae* (Ratz.) in Switzerland, Germany and France, was studied during 1950–1952. The present work is a part of the research on the complex problem of factors in the control of the Balsam Woolly Aphid in Canada.

The morphology of both the larva and the adult has been studied. Some information has been provided on the probable distribution of the species.

P. impexus has only one generation a year. The eggs are deposited during the late summer or early autumn on infested trees and the larvae hatch in April. The larvae develop and adults appear in May. The adults of the new generation are to be found in June together with adults of the old generation. In the biology, particular attention has been directed to the diet of the insect in each of its stages, in order to establish the value of the species from the standpoint of biological control.

Two new species of Hymenopterous parasites were found in Switzerland and in Germany, *Scymnophagus mesnili* Ferr., a parasite of pupae, and *Centistes scymni* Ferr., a parasite of the imagines. The life history of these species has been briefly studied. A cephaline gregarine species was noted in the mesenteron of adults of *P. impexus* and a nematode in the abdominal cavity of a female. The two Hymenopterous species provide an important limiting factor in the increase of the population of *P. impexus*.

Chrysopa ventralis Curt., *Syrphus arcuatus* (Fall.) and *Cnemodon latitarsis* Egg. are mentioned, acting as predators of *P. impexus* larvae and pupae.

The organisation of the mass-rearing of *P. impexus* in Europe as well as the shipping of the insects to Canada in special wooden boxes completes the study.

Acknowledgements.

The present study was undertaken at the European Laboratory of the Commonwealth Institute of Biological Control, Feldmeilen, Switzerland. I wish to express my deepest gratitude for the expert guidance and teaching provided during the past three years by Prof. L. P. Mesnil, in charge of the Laboratory. I am especially indebted to Prof. Dr. P. Bovey, of the Institute of Entomology of the Swiss Federal Institute for Technology, Zurich, who has been good enough to accept the present study as a doctoral thesis and has shown consistent interest and given valuable advice during the course of the investigations.

Further thanks are also extended to the following: Dr. W. R. Thompson, Director of the Commonwealth Institute of Biological Control, Ottawa, Canada; Dr. H. C. Coppel, Dominion Parasite Laboratory, Belleville, Ontario, Canada, who assisted in revising the English manuscript; Dr. Charles Ferrière, of the Natural History Museum, Geneva, and Mr. R. Hinz, Hanover, Germany, for determinations of the Hymenopterous parasites; Dr. J. Franz, German Sub-station of our Laboratory, Munich; Forest Inspector Ing. A. Marthaler, Zurich, and all those individuals who in various ways assisted during the study.

References.

Allegre, C. F. (1948). Contribution to the life history of a Gregarine parasitic in grasshoppers.—Trans. Amer. micr. Soc., **67,** pp. 211–226.

Annand, P. N. (1928). A contribution toward a monograph of the Adelginae (Phylloxeridae) of North America.—Stanford Univ. Publ. (Biol. Sci.), **6,** no. 1, pp. 1–146.

Balch, R. E. (1952). Studies of the Balsam Woolly Aphid, *Adelges piceae* (Ratz.) (Homoptera: Phylloxeridae) and its effects on balsam fir, *Abies balsamea* (L.) Mill.—Publ. Dep. Agric. Can., no. 867, 76 pp.

Baudi, F. (1889). Catalogo dei Coleotteri del Piemonte.—Ann. Accad. Agric. Torino, **32,** p. 215.

Binaghi, G. (1941). Gli stadi preimaginali del *Pullus auritus* Thunb. e dello *Scymnus rufipes* Fabr. Morfologia, notizie ecologiche ed apparati genitali (Col. Coccinellidae).—Mem. Soc. ent. ital., **20,** pp. 148–161.

Börner, C. (1952). Europae centralis Aphides. Die Blattläuse Mitteleuropas: Namen, Synonyme, Wirtspflanzen, Generationszyklen.—Schr. Thüring. Land.Arb.Gemeinsch. Heilpflanzenk. Weimar, pt. 4 (Mitt. Thüring. bot. Ges. Beih. 3), 484 pp.

Böving, A. (1917). A generic synopsis of the Coccinellid larvae in the United States National Museum, with a description of the larva of *Hyperaspis binotata* Say.—Proc. U.S. nat. Mus., **51,** pp. 621–650.

Capra, F. (1927). Aggiunte e correzioni al Catalogus Coleopterorum Regionis Palaearcticae—Endomychidae e Coccinellidae.—Boll. Soc. ent. ital., **59,** pp. 152–160.

Chapman, R. N. (1931). Animal ecology.—464 pp., New York, McGraw-Hill.

Clausen, C. P. (1940). Entomophagous insects.—688 pp., New York, McGraw-Hill.

Colyer, C. N. (1952). Notes on the life-histories of the British species of *Phalacrotophora* Enderlein (Dipt., Phoridae).—Ent. mon. Mag., **88,** pp. 135–139.

Czerny, L. (1936). Chamaemyiidae (Ochthophilidae) *in* Lindner, E.—Flieg. pal. Reg., **103,** 24 pp.

Davidson, W. M. (1923). Biology of *Scymnus nubes* Casey (Coleoptera; Coccinellidae).—Trans. Amer. ent. Soc., **49,** pp. 155–163.

van Dinther, J. B. M. (1951). Twee Coccinellidae als roofvijanden van *Dreyfusia piceae* Ratz.—Tijdschr. Ent., **94,** pp. 169–188.

van Emden, F. I. (1949). Larvae of British beetles, VII. (Coccinellidae).—Ent. mon. Mag., **85,** pp. 265–283.

Escherich, K. (1942). Die Forstinsekten Mitteleuropas, **5,** pp. 647–648. Berlin, Parey.

Franz, J. (1950). Biologische Bekämpfung der Tannenlaus.—Allg. Forstz., **5,** pp. 212–213.

Franz, J. (1951*a*). Möglichkeiten und Grenzen der biologischen Schädlingsbekämpfung.—Pflanzenschutz, **3,** pp. 100–102.

Franz, J. (1951*b*). Schädlingsbekämpfung ohne Gift—Europa hilft Amerika.—Umschau, **1951,** pt. 19.

Gage, J. H. (1921). The larvae of the Coccinellidae.—Ill. biol. Monogr., **6,** pp. 233–294.

Graham, S. A. (1939). Principles of forest entomology.—2nd edn., 410 pp. New York, McGraw-Hill.

Hofmann, C. (1938). Freilandstudien über Auftreten, Bionomie, Oekologie und Epidemiologie der Weisstannenlaus *Dreyfusia* (*Chermes*) *nüsslini* C.B.—Z. angew. Ent., **25,** pp. 1–56.

Kamal, M. (1951). The biological control of the Cotton Leaf-worm (*Prodenia litura* E.) in Egypt.—Bull. Soc. Fouad 1er Ent., **35,** pp. 221–270.

Korschefsky, R. (1931). Coccinellidae. I.—In Junk, W. Coleopt. Cat., Berl., **118,** 224 pp.

Kuhnt, P. (1913). Illustrierte Bestimmungstabellen der Käfer Deutschlands.—1138 pp. Stuttgart.

Kurdjumov [Kurdyumov'], N. V. (1912). Hyménoptères-parasites nouveaux ou peu connus.—Rev. russe Ent., **12,** pp. 223–240.

Langeron, M. (1949). Précis de microscopie. Paris.

Luigioni, P. (1929). I Coleotteri d'Italia. Catalogo sinonimico-topografico-bibliografico.—Mem. Accad. Nuovi Lincei, (2) **13,** 1159 pp.

Marchal, P. (1913). Contribution à l'étude de la biologie des *Chermes*.—Ann. Sci. nat. (Zool.), (9) **18,** pp. 153–385.

Mulsant, M. E. (1850). Species des Coléoptères trimères sécuripalpes.—Ann. Sci. phys. nat. Lyon, (2) **2,** pp. 979–980.

Parker, H. L. (1949). The handling, transporting, packing and shipping of insects, particularly parasites and predators.—*in* Les bases scientifiques d'une organisation internationale pour la lutte biologique.—[Publ.] Un. int. Sci. biol., (B) no. 5, pp. 121–127.

Porta, A. (1929). Fauna Coleopterorum Italica. III. Diversicornia.—466 pp. Piacenza.

Reitter, E. (1911). Fauna Germanica, **3**, 436 pp. Stuttgart.

Romeis, B. (1948). Mikroskopische Technik.—München.

Sainte-Claire Deville, J. (1935–38). Catalogue raisonné des Coléoptères de France.—Abeille, Paris, **36,** p. 291.

Schatzmayr, A. (1943). Appunti coleotterologici X.—Natura, Milano, **34,** pp. 132–139.

Schaufuss, C. (1916). Calwer's Käferbuch. Einführung in die Kenntnis der Käfer Europas, 6th edn., **1,** 709 pp. Stuttgart.

Schilder, F. A. & Schilder, M. (1928). Die Nahrung der Coccinellidae und ihre Beziehung zur Verwandtschaft der Arten.—Arb. biol. Reichsanst., Berl., **16,** pp. 213–282.

Schneider, F. (1948). Das biologische Gleichgewicht und die chemische Schädlingsbekämpfung.—Landw. Vortr., Frauenfeld, **16,** pp. 52–61.

SCHNEIDER, F. (1950*a*). Die Entwicklung des Syrphidenparasiten *Diplazon fissorius* Grav. (Hym. Ichneum.) in uni-, oligo- und polyvoltinen Wirten und sein Verhalten bei parasitärer Aktivierung der Diapauselarven durch *Diplazon pectoratorius* Grav.—Mitt. Schweiz. ent. Ges., **23**, pp. 155–194.

SCHNEIDER, F. (1950*b*). Die Abwehrreaktion des Insektenblutes und ihre Beeinflussung durch die Parasiten.—Vjschr. naturf. Ges. Zürich, **95**, pp. 22–44.

SCHNEIDER-ORELLI, O. (1944). Zur Schädigung der Weisstanne durch Trieb- und Rindenläuse (*Dreyfusia*).—Schweiz. Z. Forstw., **1944**, no. 1, repr. pp. 1–11.

SCHNEIDER-ORELLI, O. (1945). Weitere *Dreyfusia*-Untersuchungen.—Mitt. schweiz. Anst. forstl. Versuchsw., **24**, pp. 103–132.

SCHNEIDER-ORELLI, O. (1949). Richtlinien zur Bekämpfung der Weisstannenläuse *Dreyfusia nüsslini* und *Dreyfusia piceae* für 1949.—Schweiz. Z. Forstw., **1949**, no. 7, repr. 4 pp.

SCHNEIDER-ORELLI, O. (1950). Der gegenwärtige Stand der schweizerischen Untersuchungen über *Dreyfusia nüsslini*.—Mitt. schweiz. Anst. forstl. Versuchsw., **26**, pp. 837–860.

SÉGUY, E. (1934). Diptères (Brachycères). (Muscidae Acalypterae et Scatophagidae).—Faune Fr., Paris, **28**, pp. 360–361.

SNODGRASS, R. E. (1935). Principles of insect morphology.—667 pp. New York, McGraw-Hill.

STEINHAUS, E. A. (1946). Insect microbiology.—763 pp. New York, Comstock.

STEINHAUS, E. A. (1949). Principles of insect pathology.—757 pp. New York, McGraw-Hill.

STRICKLAND, C. (1912). *Agrippina bona* nov. gen. et nov. sp. representing a new family of Gregarines.—Parasitology, **5**, pp. 97–108.

SZELÉNYI, G. (1942). Ueber die Chalcididen-Gattung *Pachyneuron* Walk. (Hymen.).—Zbl. ges. Forstw., **68**, pp. 93–105.

TRÄGÅRDH, I. (1931). Zwei forstentomologisch wichtige Fliegen.—Z. angew. Ent., **18**, pp. 672–690.

VINCENT, M. (1922). On the life history of a new Gregarine*Pyxinia anobii* n.sp., intestinal parasite of *Anobium paniceum* L. (Coleoptera).—Parasitology, **14**, pp. 299–306.

WEISE, J. (1884). Dtsch. ent. Z., **28**, p. 424.

WENYON, C. M. (1926). Protozoology, **2**, p. 1138. London.

WILSON, F. (1938). Notes on the insect enemies of *Chermes* with particular reference to *Pineus pini*, Koch, and *Pineus strobi*, Hartig.—Bull. ent. Res., **29**, pp. 373–389.

WILSON, J. W. (1927). The male genital tube of some of the species of the genus *Scymnus* (Coleoptera, fam. Coccinellidae).—Psyche, **34**, pp. 167–170.

ANOPHELES AND MALARIA AT ANEITYUM, NEW HEBRIDES.*

By Marshall Laird, M.Sc., Ph.D.†

Aneityum, the most southerly island of the New Hebrides, lies in Latitude 20°12′ South and Longitude 169°47′ East. An almost circular island of volcanic origin, it is some ten miles across from east to west, and about nine miles from north to south. The interior is mountainous, with wooded peaks rising to 2,788 feet. There are numerous streams with deep and often swampy valleys, and extensive coastal lowlands.

This island is at the perimeter of the malarious zone of the south-west Pacific, a zone generally understood to be bounded by the Latitude of 20° South and Longitude of 170° East. A study of the literature discloses a difference of opinion as to whether or not Aneityum itself is malarious. Thus Buxton and Hopkins (1927) stated that malaria occurs on the island, while Hérivaux and others (1938) asserted that it does not. Buxton himself did not visit Aneityum, and he indicated that his information was derived from a medical missionary who had spent some time there. Although, as is shown in the following section, the weight of presumptive evidence has indicated that malaria is endemic on the island, there are no previous records either of the finding of *Anopheles* or of a blood-smear survey at Aneityum.

Historical.

Captain James Cook discovered Aneityum in 1774 during his second voyage to the South Seas, but did not land there. During the earlier years of the nineteenth century sporadic visits were made by European traders, and in 1840 H.M.S. *Sulphur* sailed close to the island. Furnas (1950) erroneously stated that Captain Belcher of this ship rescued a Samoan missionary party "suffering more or less from fever and ague" from Aneityum. This party was in actual fact encountered at (and not rescued from) Port Resolution, Tanna (Belcher, 1843, pp. 57–59).

The arrival of Catholic and Presbyterian missionaries in 1848 led to the first references to malaria at Aneityum. Referring to the personnel of the Catholic establishment, Inglis (1887) stated "There was a lurking enemy near them which they did not suspect. There was a large swamp behind their home over which the trade-wind blew, and wafted the invisible and impalpable malaria into their dwelling. The result was that, in a comparatively short time, one after another of the party was laid down with fever and ague." Being no respecter of sects, malaria also affected the Presbyterians. Inglis declared that "When I visited Aneityum in the *Havannah* in 1850, Mr. Geddie came on board, accompanied by a Raratongan teacher. He had been suffering some months from fever and ague and was very much reduced, and was looking very ill; the teacher was still worse, and died a few weeks thereafter." According to Hutton (1874), Mr. Geddie's sickness took the form of "a low intermittent fever". In due course, "with the exception of Mrs. Geddie, nearly every member of the mission had long and severe attacks of fever and ague, the one outstanding disease of Aneityum and of the New Hebrides" (Inglis, 1887).

---

* These studies form part of a project initiated by the Royal New Zealand Air Force and supported by a grant from the N.Z. Department of Scientific and Industrial Research. Their publication is authorised by the Chief of Air Staff, RNZAF.

† Medical Branch, RNZAF.

Despite the facts that the early missionaries on Aneityum knew nothing of the malarial organisms nor of their means of transmission, and that they could well have included other diseases than malaria within the definitions of their "intermittent fevers" and "ague", it seems likely, then, that the island has been malarious at least from the initial period of settlement by Europeans.

Malaria has been counted among the factors concerned with population decline in various Pacific island groups including the New Hebrides (*e.g.*, Espiritu Santo; Baker, 1928). The Aneityumese suffered appallingly heavy casualties in epidemics of such introduced diseases as measles following their first contacts with Europeans. Their population, initially estimated as at least 12,000 (Inglis, 1890), had fallen to 1,488 by 1874 and to 1,279 by 1878 (Steel, 1880). Inglis (1890) observed that in consequence of such drastic reductions in the population "a large proportion of the land was thrown out of cultivation, and a large amount of swamp land, instead of being finely cultivated food-producing gardens, fell into stagnant marshes, largely increasing the fever-producing malaria." Although this suggestion envisaged merely an augmentation of supposedly noxious marsh effluviae, it is very possible that an increase in the malaria rate did take place in consequence of a rise in the anopheline population due to intensified breeding in neglected taro grounds. Such an increase in the incidence of malaria would have played its part in reducing the resistance of the natives to epidemic and other diseases brought by Europeans. The population decline, whether or not hastened by malaria, has continued steadily, and today the census of Aneityumese has fallen to the vicinity of 150.

Material and Methods.

A visit was paid to Aneityum from 3rd to 6th August 1952, a field laboratory being established at the headquarters of the Aneityum Logging Company, Anelgauhat, near the site of the former missions. Nearby mosquito larval habitats were investigated, morning collections of blooded mosquitos were made from torn and badly hung bed nets in native huts, and a blood-smear survey was undertaken. All the blood preparations were stained with Giemsa, a thick and a thin film being made from each of the individuals concerned. In order that additional material could be obtained from any natives found to be harbouring *Plasmodium*, all smears were examined on the spot by means of a Zeiss-Winkel GF525 microscope having an integral illuminant powered by a 6v. car battery.

Results of the Survey.

All developmental stages of *Anopheles farauti* Laveran, 1902, were found in abundance, particularly in taro swamps. By far the greater number of larvae had the tubercles of the inner and centre shoulder hairs joined to form a single plate, though in some they were separate on one side and joined on the other, as noted for this species by Lee and Woodhill (1944). Larvae were particularly common in taro swamp irrigation channels, where masses of *Spirogyra* and emergent and marginal vegetation afforded them a degree of protection from both direct sunlight and predators. The time available was insufficient for accurate figures of larval density to be obtained, but 100 dips with a 200 cc. ladle yielded an average of two fourth-instar larvae per dip. A few resting males and females of *A. farauti*, probably recently emerged, were disturbed from marginal vegetation bordering the larval habitats. Mosquitos of other genera collected at the same time will be discussed elsewhere.

Blooded females of *A. farauti* were collected from bed nets in native huts, as many as 17 being found in a single net. All the adults examined were typical of their species in having the proboscis entirely dark-scaled (Lee & Woodhill, 1944). Females of *Culex annulirostris* Skuse, 1889, were often present as well, and in huts more than a mile distant from the nearest taro swamp this species was the only one present.

The results of blood examinations of 45 natives, almost a third of the present population, are detailed in Table I.

TABLE I.

Analysis of blood-smear examinations.

Age (years)	Number without parasites	Number with *P. falciparum*	Number with *P. vivax*	Number with *P. malariae*	Total
Under 1 ..	3 + (1)	0	(1)	0	5
1—4 ..	6 + (1)	0	(1)	2	10
5—9 ..	10 + (2)	0	0	3	15
10–14 ..	2 + (3)	0	0	0	5
15–19 ..	0	0	0	0	0
20–29 ..	(5)	0	0	0	5
30–39 ..	(3)	0	0	0	3
40+ ..	(2)	0	0	0	2
Total	21 + (17)	0	(2)	5	45

The bracketed numbers indicate natives who had at some time been away from Aneityum.

Although, as the above Table shows, both *Plasmodium vivax* and *P. malariae* were recorded, *P. falciparum*, which is of common occurrence in the central and northern New Hebrides (Levine & Harper, 1947), was not found. Proportionately more children than adults were examined, both because it was felt that blood smears from children would be more likely to contain malaria parasites than those from adults and because most of the older natives had been to other islands of the group; some, indeed, had travelled quite widely on board trading vessels. None of the five children parasitised by *P. malariae* had ever left Aneityum. On the other hand, both of the children infected with *P. vivax* had accompanied their parents on visits to the island of Tanna, which lies about 40 miles north-west of Aneityum. Buxton and Hopkins (1927) published the results of a blood-smear survey at Whitesands, Tanna, where 3 out of 33 children examined were found to have benign tertian malaria (*P. falciparum* was not recorded). Whether or not the Aneityumese children concerned had become infected at Tanna, and although *P. vivax* was not recorded from children who had never been away from Aneityum, the fact remains that a reservoir of infection is available to the local Anophelines.

Splenomegaly is not so evident in quartan as in benign tertian malaria (Kitchen, 1949). None of the Aneityumese children infected with *P. malariae* had noticeably enlarged spleens, and it is certain that had the present survey been based on the splenic index instead of on blood examinations the occurrence of malaria on the island would have been overlooked.

Discussion.

There is no previous record of endemic quartan malaria from the New Hebrides. *P. malariae* is notable for the patchiness of its distribution. As recently as 1924 this parasite was recorded as being only rarely recognised in Papua, and had not been reported from as far south as the Solomon Islands (Cumpston, 1926). During a period spent in the latter group during 1927–34, however, Sayers (1943) found a *P. malariae* rate of 18 per cent. among 741 parasite-positive cases of clinical malaria.

Buxton and Hopkins (1927) reported the presence of both *P. falciparum* and *P. vivax* during their researches in the New Hebrides in 1924. Levine and Harper (1947) gave an analysis of data amassed by the United States military organisations in the south-west Pacific during World War II. These authors stated that 4,000 natives were examined for *Plasmodium* at Efate, central New Hebrides, and the same number at Espiritu Santo in the north. A total of 205 positive cases were recorded at Efate, where only *P. falciparum* and *P. vivax* were found. Of 486 infected natives at Espiritu Santo, however, 0·5 per cent. were positive for *P. malariae*. Unfortunately, Levine and Harper failed to note whether the two or three natives concerned had ever visited the Solomons or other Pacific islands where quartan malaria is endemic. Finally, in his recent geographical consideration of quartan malaria, Brumpt (1949) stated that this disease does not extend to the New Hebrides.

While no information was sought regarding the vector of *P. malariae* at Aneityum, the answer appears to be self-evident; for no Anophelines other than *A. farauti* are known from the New Hebrides, and all those collected at the island were in every respect typical of this species. *A. farauti* has not previously been known to be a vector of *P. malariae*, the only experimentally proven vector of this parasite in Australasia being the closely related *Anopheles punctulatus* Dönitz, 1901 (Mackerras & Ercole, 1948).

Brumpt (1949) pointed out that "in a country where a single species of *Anopheles* transmits all the species of human plasmodia, *P. malariae* infections are highly localised in certain localities, where they may be especially numerous." This generalisation thus holds good for the New Hebrides, although Brumpt, in applying it to the Pacific, erred in assuming *A. punctulatus* to be the only Anopheline present throughout this area.

Summary.

Aneityum is the only Pacific island south of Latitude 20°S. from which Anophelines and autochthonous malaria have yet been reported. Both *Plasmodium vivax* and *P. malariae* were found there, the former species only being detected in the blood of children who had visited the nearby island of Tanna and the latter in that of children who had never left Aneityum. Autochthonous quartan malaria has not previously been reported from the New Hebrides. In the absence of any other Anophelines from this group, it must be assumed that *Anopheles farauti* Laveran is the vector of *P. malariae* at Aneityum.

Acknowledgements.

It is my pleasure to record the ready co-operation received from the Commanding Officer, RNZAF Station, Lauthala Bay, Fiji; from the Officer Commanding and personnel of No. 5 (N.Z.) Flying Boat Squadron, a Catalina aircraft of which was employed for the visit to Aneityum; from Mr. A. C. Stevenson of the Aneityum Logging Company; and from my wife, whose assistance in the field helped to make possible the success of so short a survey.

References.

Baker, J. R. (1928). Depopulation in Espiritu Santo, New Hebrides.—J. R. anthrop. Inst., **58**, pp. 279–303.

BELCHER, Sir E. (1843). Narrative of a voyage round the world, performed in H.M.S. Sulphur, during the years 1836–1842, **2,** 474 pp. London, Colburn.

BRUMPT, E. (1949). The human parasites of the genus *Plasmodium*.—*In* Boyd, M. F. *Ed.* Malariology, **1,** pp. 65–121. Philadelphia, Pa., Saunders.

BUXTON, P. A. & HOPKINS, G. H. E. (1927). Malaria and filariasis in the New Hebrides.—Mem. Lond. Sch. Hyg. trop. Med., no. 1, appdx. 2, pp. 225–237.

CUMPSTON, J. H. L. (1926). Disease distribution in the Pacific basin.—Proc. Pan-Pacif. Sci. Congr. 1923, **2,** pp. 1400–1407.

FURNAS, J. C. (1950). The anatomy of paradise.—542 pp. London, Gollancz.

HÉRIVAUX, A., RONCIN, R. & DAO VAN THAI (1938). Paludisme.—Rep. Hlth Serv. New Hebrides, 1937–38.

HUTTON, J. (1874). Missionary life in the South Seas.—346 pp. London, King.

INGLIS, J. (1887). In the New Hebrides.—352 pp. London, Nelson.

INGLIS, J. (1890). Bible illustrations from the New Hebrides.—356 pp. London, Nelson.

KITCHEN, S. F. (1949). Quartan malaria.—*In* Boyd, M. F. *Ed.* Malariology, **2,** pp. 1017–1026. Philadelphia, Pa., Saunders.

LEE, D. J. & WOODHILL, A. R. (1944). The Anopheline mosquitoes of the Australasian Region.—Monogr. Dep. Zool. Univ. Sydney, no. 2, 209 pp.

LEVINE, N. D. & HARPER, P. (1947). Malaria and other insect-borne diseases in the South Pacific campaign, 1942–1945. IV. Parasitological observations on malaria in natives and troops, and on filariasis in natives.—Amer. J. trop. Med., **27,** no. 3 suppl., pp. 119–128.

MACKERRAS, M. J. & ERCOLE, Q. N. (1948). Observations on the life-cycle of *Plasmodium malariae*.—Aust. J. exp. Biol. med. Sci., **26,** pp. 515–519.

SAYERS, E. G. (1943). Malaria in the South Pacific with special reference to the Solomon Islands.—N.Z. Govt. Print. Off.

STEEL, R. (1880). The New Hebrides and Christian missions.—485 pp. London, Nisbet.

A MOSQUITO SURVEY IN NEW CALEDONIA AND THE BELEP ISLANDS, WITH NEW LOCALITY RECORDS FOR TWO SPECIES OF *CULEX*.*

By Marshall Laird, M.Sc., Ph.D.†

The archipelago made up by New Caledonia, the Belep Islands to the north-west and the Isle of Pines to the south-east, is bounded by Latitudes 19°30′ and 22°40′ South and Longitudes 163°35′ and 167°35′ East. New Caledonia itself is 248 miles in length and averages 30 miles in breadth. Its northern tip and the off-lying island of Baaba are in the same latitude as Aneityum, the most southerly Pacific island known to be malarious (Laird, 1954), which is some 360 miles to the east. The Belep Islands are positioned within the barrier reefs which trend north-west from New Caledonia. They extend for 23 miles more or less in line with the mainland ridge, from which they are separated by some 30 miles of sea. Art, the largest island, rises to an altitude of 728 feet. The Belep group has no European settlements other than the Mission Station at Uala, on the western coast of Art Island, where virtually all of the 550 natives (Melanesians and part Melanesians) are congregated.

There is no evidence that *Anopheles* or autochthonous malaria have ever been encountered in any of the islands of the New Caledonian archipelago. Mumford (1942) and Perry (1950) have reviewed the relevant literature, the latter author asserting that this island was still free from *Anopheles* and malaria at the end of active military occupation in 1946.

Comprehensive anti-anopheline measures in the area ceased with the withdrawal of Allied entomological control units. At the same time, New Caledonia remained more exposed to airborne introductions of dangerous insects than it had been in pre-war days; for air links were developed with countries such as the New Hebrides, Indo-China and Australia, in which occur species of *Anopheles*. The present flying-boat link with the New Hebrides brings Noumea, the capital of New Caledonia, within a very few hours flying time of the malarious islands of Efate and Espiritu Santo.

Buxton (1926) stated that in general all the islands between the Equator and 20° S., and New Guinea and 170° E., are malarious, the only exceptions being the Belep Islands "and a very few minute islands such as Tucopia." However, there is no indication in the literature as to what mosquitos occur in the Belep group, no mention being made of these islands by Williams (1943) and Perry (1950) in their accounts of the Culicidae of New Caledonia.

It was with the objects of ascertaining whether Anophelines have appeared in New Caledonia since the end of the war, and of undertaking mosquito- and haematozoan-surveys in the Belep Islands, that the reconnaissance discussed hereunder was carried out during November and December 1952.

The Culicidae of the New Caledonian Mainland.

Our knowledge of this fauna has been most recently summarised by Williams (1943) and Perry (1950). The latter author's list of the species recorded during the wartime surveys includes all 13 of the mosquitos known from the island prior to the present investigation:—

---

* These studies form part of a project initiated by the Royal New Zealand Air Force and supported by a grant from the N.Z. Department of Scientific and Industrial Research. Their publication is authorised by the Chief of Air Staff, RNZAF.

† Medical Branch, RNZAF.

Tripteroides (Mimeteomyia) caledonica (Edwards)

Mansonia (Coquillettidia) crassipes (van der Wulp)

Aëdes (Mucidus) alternans (Westwood)
Aëdes (Mucidus) kermorganti (Laveran)
Aëdes (Ochlerotatus) vigilax (Skuse)
Aëdes (Finlaya) notoscriptus (Skuse)
Aëdes (Stegomyia) aegypti (L.)
Aëdes (Aëdimorphus) vexans (Meigen)

Culex (Culex) annulirostris Skuse
Culex (Culex) sitiens Wiedemann
Culex (Culex) pipiens fatigans Wiedemann* = (*C. quinquefasciatus* Say)
Culex (Culex) basicinctus Edwards
Culex (Neoculex) pseudomelanoconia Theobald

All but three of these species, *M. crassipes*, *A. alternans* and *A. kermorganti*, were collected in the course of a larval survey extending from Noumea along the western coast to Poum in the far north, during the periods 15th–24th November and 3rd–11th December 1952. As regards *M. crassipes*, larval *Mansonia*, which attach themselves to plant tissues underwater, were not specially searched for. That *A. alternans* was not collected might be due to seasonal factors. Cooling (1924) indicated that this species is seldom found in Queensland outside the period of influence of the king tide (latter part of January —middle of March). *A. alternans* breeds in salt marshes, where its larvae prey upon those of *A. vigilax* and *C. sitiens* (Cooling, 1924); and both of these species were found in all the suitable larval habitats examined. Williams (1943), who worked in New Caledonia during the period August–November 1940, also failed to find *A. alternans*, although he too collected *A. vigilax* and *C. sitiens* on many occasions.

It should be noted that there is some doubt concerning the identity of *A. kermorganti*, the larvae of which have not been described (although Perry, 1950, included it among the mosquitos recorded in wartime larval surveys). Edwards (1922) was of the opinion that this species might merely be a form of *A. alternans*.

The following larval associations were noticed: *A. vigilax* and *C. sitiens* (four times), *A. vexans* and *C. annulirostris* (once), *C. annulirostris* and *C. pipiens fatigans* (once), *C. annulirostris* and *C. bitaeniorhynchus* (twice).

In all the coastal areas visited, *A. vigilax* was by far the most abundant and most troublesome day-biting mosquito. It readily bites through clothing, even when exposed to bright sunshine. On one occasion, while in the north of the country, my wife and I were bitten about the head and shoulders while swimming about fifteen yards from the banks of the Kone river on a hot, sunny afternoon. Fortunately, this species is very sensitive to dimethyl phthalate repellents. *C. annulirostris* was the most numerous and widely-distributed night-biter at the time of the survey. *C. sitiens* and *A. vexans* were sometimes locally abundant in the vicinity of their breeding places, the former species particularly so at Gatope village (on the coast near Voh) and the latter one at Tontouta Airport, where its larvae were common in ponded drainage ditches. Many adults of *C. pipiens fatigans* (both sexes) were collected in the passenger waiting room at Tontouta on 18th November 1952, although a prolonged search failed to reveal any larvae in the vicinity. No adults of either *A. notoscriptus* or *A. aegypti* were found outside of the Noumea area, but these mosquitos, particularly the latter one, are said to be common domestic pests in the town itself. The only other species recognised in the field in the adult state was *T. caledonica*, a single female of which was captured at light at Anse Vata, Noumea, at 21.30 hrs. on 22.xi.1952.

---

* See note on p. 293.

Williams (1943) and Perry (1950) agreed as to the major importance of *A. vigilax* as a pest mosquito in New Caledonia. However, the latter author failed to comment on the prevalence of *C. annulirostris* adults, although he recorded larvae from fresh or stagnant water in ponds, road ruts and artificial catchments, while Williams, Theobald (1913) and Edwards (1922) did not record this species at all. The lack of earlier information concerning this mosquito in New Caledonia is surprising, for *C. annulirostris* was second only to *A. vigilax* in pest significance during the present survey. Its developmental stages were found in freshwater ground pools of various kinds both on the mainland (Table I) and in the Belep Islands (p. 291) more frequently than were those of any other mosquito.

With two exceptions, the larvae of the mosquitos previously known from the island correspond with the descriptions published by Lee (An atlas of the mosquito larvae of the Australasian region. Tribes Megarhinini and Culicini.—119 pp. Aust. milit. Forces H.Q., 1944). The siphonal detail of my examples

TABLE I.

Synopsis of larval records.

Species	Localities	Habitats	No. of times collected*
T. caledonica	Noumea	Tree-hole	1
A. vigilax	Noumea, Tontouta, Voh, Koumac, Poum	Mangrove swamps, brackish and tidal pools	8
A. notoscriptus	Noumea	Tin can	1
A. aegypti	Noumea	Water tanks	2
A. vexans	Noumea, Tontouta	Ponded ditches	2
C. annulirostris	Noumea, Tontouta, Voh-Koumac-Poum	Ponded ditches, hoof-print pools, swamps, road ruts, etc.	9
C. sitiens	Noumea, Voh, Koumac	Mangrove swamps, brackish and tidal pools	4
C. pipiens fatigans	Poum	Water drum, swamp	2
C. basicinctus	Voh	In algae at edges of Temala river	2
C. pseudomelanoconia	Near Bouerabate, far north	At edges of a ponded, rocky creek	1
	First record from New Caledonia		
Culex (*Culex*) *bitaeniorhynchus* Giles	Anse Vata (Noumea)	In masses of *Spirogyra* in ponded ditches	2

* The total number of individual collections (26) was less than the sum of these figures indicates, as more than one species of mosquito sometimes utilised the same larval habitat. Each collection was a comprehensive one embracing all aspects of the biology of the water body concerned, an average of an hour being spent in the examination of each breeding place. Similar studies were made of a number of water bodies which altogether lacked Culicidae. A detailed consideration of the data gathered will be published at the conclusion of the studies at present in progress, as a contribution to Pacific mosquito ecology.

of *C. pseudomelanoconia* differs considerably from that of the Australian larvae described and figured by Lee, but agrees substantially with that of the New Caledonian material discussed by Williams (1943). The larvae figured by Lee (his Pl. 85) has a siphonal index of 4·7 : 1, the siphon having a medial dark band, whereas that illustrated by Williams (his fig. 12a) has a long and slender siphon (index 7·3 : 1) lacking such a band. As is shown in fig. 4, the siphon of the larvae which I collected near Bouerabate is of similar length-breadth ratio to that figured by Williams, but has a prominent dark band medially—although this band is darker in some larvae than in others, and may disappear altogether in alcohol-preserved specimens. The pecten teeth, which Lee illustrated as only slightly serrated, are, as Williams figured them, prominently multi-dentate (fig. 2). Williams failed to describe the characteristics of the head, but, according to Lee, head hair B is very long and single, while C and d are very short and branched. In the Bouerabate larvae head hair B is double, C is single and about half the length of B, while d is comparatively short and branched (fig. 1).

The second mosquito showing marked variance from Lee's account is *C. annulirostris*. Larvae of this species collected in New Caledonia, particularly those from natural swamps of a permanent nature, frequently have a much longer and more slender siphon than the ones described by Lee (his Pl. 75, siphonal index about 7 : 1). Their siphonal index reaches 10 : 1, and there are often seven instead of the customary six siphonal hairs; while the anal gills, normally about three-quarters the length of the saddle, may be appreciably longer than this structure. Adults reared from such larvae do not differ from typical *C. annulirostris*. Perry (1946) reported a similar variation of the larvae of this species in the New Hebrides, those from natural freshwater swamps having a siphonal index close to 8 : 1 in contrast to those from various ground pools of a temporary nature which possessed a short siphon having an index of from 4·5 : 1 to 6 : 1.

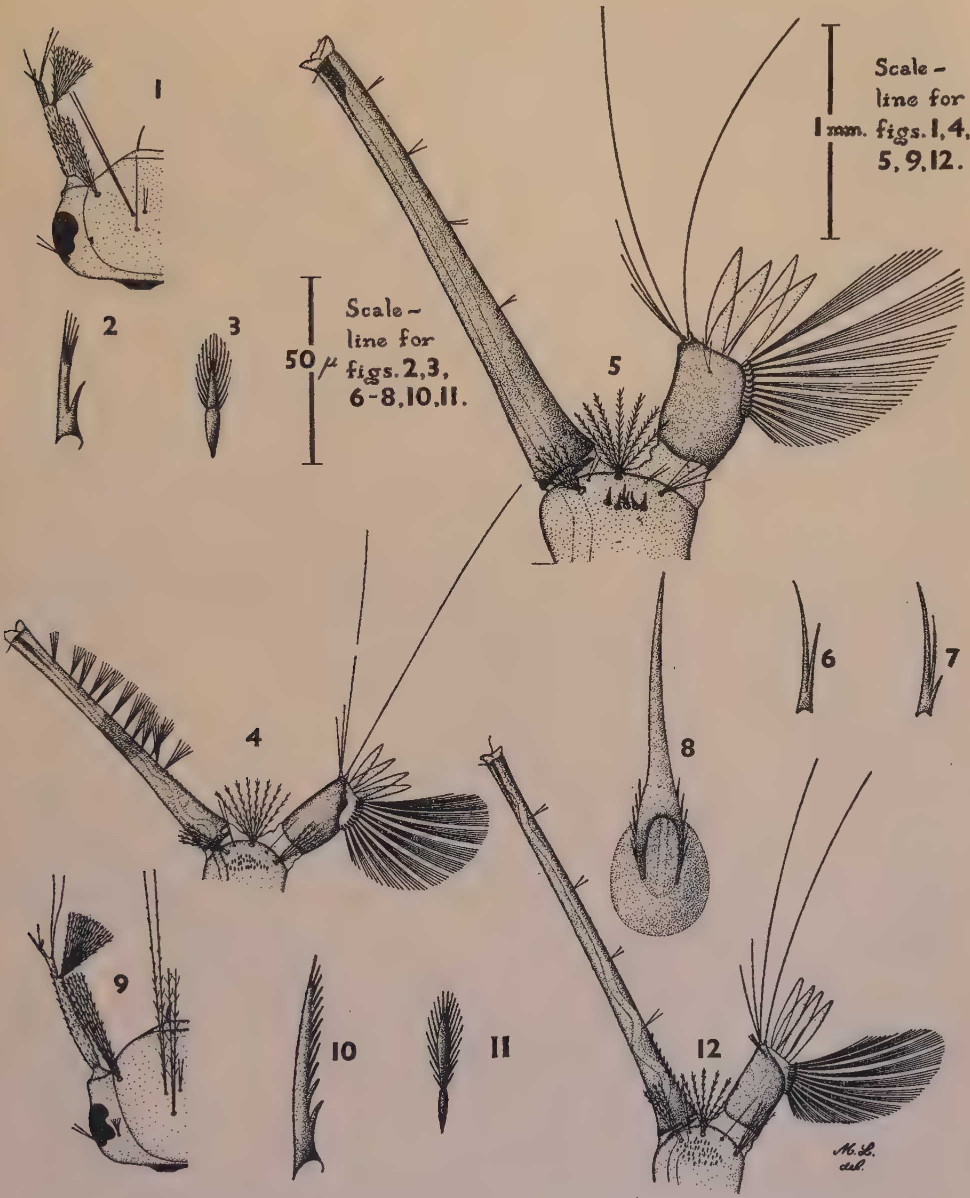
Culex (*Culex*) *bitaeniorhynchus* Giles has never before been reported from New Caledonia, nor indeed from any of the islands of the south-west Pacific. The distribution of this species was given by Lee (*loc. cit.*) as New South Wales, Northern Australia, the Oriental Region and Africa. The larvae of *C. bitaeniorhynchus* cannot be confused with those of any other Australasian mosquitos. According to Lee (*loc. cit.*) their diagnostic characters are as follows:—

> Siphon extremely long, with 4 pairs of ventro-lateral bifid hairs. Pecten inconspicuous. The most obvious character is the lateral comb, which consists of about 6 spines, each arising from a chitinous base.

All aquatic stages of *C. bitaeniorhynchus* were collected from ponded ditches at Anse Vata, Noumea, on 21.xi.1952. Larvae were abundant in clumps of *Spirogyra* at the bottom of the clear, fresh water in these ditches. The pH of the water was 8·2 (at 30°C.), and there was no overhanging vegetation at the surface, which was fully exposed to sunlight. The only other species of mosquito present was *C. annulirostris*.

As seen in the field the *bitaeniorhynchus* larvae had a very pale body with a jade green tinge. They differed from all the other species of *Culex* studied in New Caledonia in that they died instantly on immersion in 70 per cent. alcohol. Dissection revealed the gut to be crammed full with chewed-off lengths of *Spirogyra* filaments. The terminal segments, and the pecten and comb teeth, are illustrated in figs. 5–8. There are from three to seven irregularly arranged spines (fig. 8) in the lateral comb, the characteristic number being six. In all important respects the larvae from Anse Vata agree with Lee's description and figures.

C. bitaeniorhynchus was not found outside the Noumea area, although its larvae were specially searched for. The occurrence of this mosquito in the


1
Scale-
line for
1 mm. figs. 1, 4,
5, 9, 12.
2
3
Scale-
line for
50 μ figs. 2, 3,
6-8, 10, 11.
5
6
7
4
8
9
10
11
12
M.L.
del.

Figs. 1–4.—*Culex (Neoculex) pseudomelanoconia* Theobald, fourth instar: (1) head, dorsal view (left side only); (2) pecten tooth; (3) lateral comb scale; (4) terminal segments, lateral view.

Figs. 5–8.—*Culex (Culex) bitaeniorhynchus* Giles, fourth instar: (5) terminal segments, lateral view; (6) and (7) pecten teeth; (8) lateral comb scale.

Figs. 9–12.—*Culex (Lophoceratomyia) fraudatrix* Theobald, fourth instar: (9) head, dorsal view (left side only); (10) pecten tooth; (11) lateral comb scale; (12) terminal segments, lateral view.

(All figures prepared with the aid of a Zeiss-Winkel drawing apparatus, from alcohol-preserved specimens mounted in Canada balsam.)

vicinity of the capital, which received prolonged attention by Allied mosquito control during the war years, is noteworthy. Indeed, the collection localities are within a few hundred yards of a former Naval headquarters, and abandoned drip-oilers nearby testify to the control activity which once went on there. Even if this species had been overlooked in the collections discussed by Edwards (1922) and Williams (1943), it is most unlikely that such conspicuous larvae would have gone unnoticed by the wartime entomological survey teams.

It is therefore considered very likely that *C. bitaeniorhynchus* has been introduced into New Caledonia since the cessation of mosquito control activities in 1946. Such an introduction could have been made from New South Wales, as regular shipping and flying-boat services are maintained between Sydney and Noumea.

This circumstance underlines the necessity for the maintenance of efficient entomological quarantines at the ports of entry for both ships and aircraft to New Caledonia. Although the island is as yet free from *Anopheles*, breeding conditions there appear suited both to the south-west Pacific *A. farauti* Laveran and to Oriental and Indonesian species which utilise mangrove swamps as larval habitats. In the latter connection, extensive mangrove swamps occur at certain seaports, particularly at Koumac in the north, and also at Tontouta, the only airport at present used by land-based aircraft from abroad. These swamps and the adjacent salt marshes are the breeding grounds of myriads of the two brackish-water mosquitos *Aëdes vigilax* and *Culex sitiens*. In Indonesia and south-east Asia these same mosquitos occur in mangrove areas, together with *Anopheles sundaicus* (Rodenwaldt). The latter species is an important malaria vector in Indonesia and Indo-China (Puri, 1949), and that it has not yet reached the limits of its distribution is shown by its recent invasion of eastern India (Muirhead Thomson, 1951). In view of this, and the frequent air and sea traffic between Indo-China and New Caledonia by way of Indonesia, it is considered that serious attention should be paid to the problems of entomological quarantine at the ports of entry in question.

Turning now to *Anopheles farauti*, this mosquito, the most widely distributed vector of the human malarial organisms in the south-west Pacific, is abundant in the New Hebrides. In this group, its larvae are found in the same range of habitats as are those of *C. annulirostris*. Comparisons being made during the present studies have so far failed to disclose any fundamental differences in the biology or chemistry of breeding places of the latter mosquito in the New Hebrides and New Caledonia, and there are *annulirostris* larval habitats throughout the area of Noumea, the port of entry for flying boats which maintain a weekly air service with the New Hebrides and also for shipping from this group. Here again, a definite hazard appears to exist and should be met with more comprehensive preventative measures than the (not always efficient) insecticidal spraying of aircraft alone.

Investigations in the Belep Islands.

Eight days (25.xi.52–2.xii.52) were spent at Art Island, which is largely of serpentine formation. The eastern end of this island has a very arid appearance; the ochreous-red colour of its soil, which is due to the presence of quantities of iron, showing everywhere through the sparse, drought-resistant scrub. Numerous very small streams run quite steeply down to the coast, more or less at right angles to the central ridge, and there are a few short creeks subject to tidal influence. At the time of the survey, which took place at the end of the dry season, the beds of most of the smaller streams were dry, containing only scattered pools in cavities excavated by cascades during the wet season. The central spine of the island carries stretches of forest composed chiefly of niaouli

(*Melaleuca leucadendron*). Above the Mission Station at Uala, at an altitude of some 300 feet, there is a permanent pond about 80 feet across in a marshy hollow surrounded by niaouli trees. Vegetation is somewhat denser on the eastern coast, and near an old village towards the north-eastern end of the island there are stretches of mangrove swamp and a few freshwater seepage pools.

Six species of mosquitos were collected during this visit:—*T. caledonica*, *A. vigilax*, *A. vexans*, *C. annulirostris*, *C. pipiens fatigans* and *Culex* (*Lophoceratomyia*) *fraudatrix* Theobald, of these the last being recorded from the New Caledonian area for the first time.

As in New Caledonia, *C. annulirostris* was the mosquito most commonly found breeding in freshwater ground pools. Its larvae were taken in ponded stream channels and ditches, in seepage pools on the north-eastern coast, and in the permanent pond in the hills above Uala. *C. pipiens fatigans* was also plentiful, its larvae being abundant in small pools rich in organic matter in the vicinity of native dwellings. Adults of these two Culicines made up the bulk of routine night catches. *A. vigilax* was not so abundant as on the mainland, although this species was troublesome in the vicinity of the mangrove swamps on the north-eastern coast. *A. vexans* was seldom collected, and its larvae were found once only, a few in the second instar being taken from the pond above Uala in which they were living in association with *C. annulirostris*.

Several hours were spent in a fruitless search for mosquito larvae in the water held in the leaf axils of *Pandanus*. Pitcher plants (*Nepenthes* spp.), which afford a favourite larval habitat for *Tripteroides caledonica* on the mainland, were never seen on the island. On one occasion, however, larvae of this species were found, quite fortuitously, together with those of *C. fraudatrix* and *C. fatigans*. Very heavy rain, the first for some time, fell on the evening of 29th November. During the following afternoon, a number of obviously discomforted larvae were noticed at the surface of a rock pool in the bed of a small stream about a mile and a half north of Uala. The water in this pool was coloured bright yellow with suspended mud. On collection, the larvae in question proved to be those of the three species mentioned above. Although adults could not be obtained, as all the larvae died soon after they were found, no hesitation was felt, other than in the case of *C. pipiens fatigans*, in assigning these mosquitos to the species indicated.

Three of the larvae agree with the diagnosis of *Culex* (*Lophoceratomyia*) *fraudatrix* Theobald as given by Lee (*loc. cit.*) in all respects other than in the presence of a dark band just beyond the mid-point of the siphon. Perry (1946), describing the larvae of *C. fraudatrix* in the New Hebrides, stated that the siphonal band is only occasionally present, and indicated that *Culex hilli* var. *buxtoni* Edwards (which was said to have a siphon resembling that of *C. fraudatrix* but lacking a dark band) is a synonym of the former species. I have myself collected *fraudatrix* larvae lacking a siphonal band, and similar in every respect to the one under discussion, in the New Hebrides; and therefore regard the Art Island larvae (figs. 9–12) as belonging to this species.

C. fraudatrix is widely distributed from Australia to south-east Asia (Lee, *loc. cit.*), and in Melanesia has been recorded from New Guinea and New Britain to the Solomons and New Hebrides (Perry, 1946). In New Britain (Laird, 1946) and the New Hebrides its larvae are frequently found in association with those of *Anopheles farauti*.

Nineteen of the larvae of the second species of *Culex* from this pool have a stout, straight-sided siphon (index 5 : 1) bearing three pairs of ventro-lateral hair tufts and one dorso-lateral pair. The maximum width of the siphon is at the base, this being the chief larval characteristic used in the separation of *Culex* (*Culex*) *pacificus* Edwards from *C. pipiens fatigans* by Lee (*loc. cit.*), who stated that in the latter species the siphon usually has curved sides, its greatest width being about one-third from the base. On comparison of the Art Island material with *C. pacificus* larvae from the New Hebrides (the only known locality for this species), however, a point of difference is obvious. As indicated by Perry (1946) the larvae of the latter mosquito have stout and bluntly pointed setae on the basal two-thirds of the antennae, whereas in *C. pipiens fatigans* these spines are slender and tapered. As the setae concerned are in the latter condition in the Art Island larvae, it is considered that these are referable to *C. pipiens fatigans* despite the uncharacteristic shape of the siphon.

The larvae discussed above had presumably been flushed from their natural habitats further up the hillside as a result of the previous night's downpour, those of *Tripteroides caledonica* having probably been washed out of a rot-hole either in a branch overhanging the stream or in a fallen tree.

Once again no Anophelines were discovered. As a further check against the presence of such mosquitos, however, both thick and thin blood smears were taken from all the native children who had never left the Belep Islands—a total of 170, their ages ranging from a few months to seventeen years. A thorough microscopic examination of these preparations disclosed no haematozoa whatsoever (although as all the smears were made during the daytime, there is a possibility that periodic microfilariae occur but were overlooked). In view of the facts that so many children were found negative for *Plasmodium*—for at Aneityum, earlier in the 1952 dry season, 7 of 45 children examined were found to be positive (Laird, 1954)—and that no Anophelines were discovered even though all apparently suitable larval habitats encountered were thoroughly searched, it is felt that the Belep Islands, as New Caledonia itself, can be definitely considered as yet free from *Anopheles* and malaria.

Summary.

The mosquito fauna of New Caledonia and the Belep Islands is discussed, together with some features of the larval morphology of *Culex* (*Culex*) *pipiens fatigans* Wied., *C.* (*C.*) *annulirostris* Skuse and *C.* (*Neoculex*) *pseudomelanoconia* Theo. *Culex* (*C.*) *bitaeniorhynchus* Giles, herein recorded from New Caledonia for the first time, is probably a post-war introduction into the Noumea area from Australia. *Culex* (*Lophoceratomyia*) *fraudatrix* Theo., recorded from Art Island (Belep group), has not previously been known from the New Caledonian area. From the mosquito and blood-smear survey in the Belep Islands, it is concluded that these islands, like New Caledonia, are as yet free from *Anopheles* and malaria.

Acknowledgements.

The assistance of the Secretary-General and staff of the South Pacific Commission at Noumea, and of the Director and medical officers of the New Caledonian Health Service, is gratefully acknowledged, as is that of Père Yvon who made accommodation available at the Uala Mission Station, and of my wife who assisted in the field and laboratory throughout this survey.

References.

Buxton, P. A. (1926). The depopulation of the New Hebrides and other parts of Melanesia.—Trans. R. Soc. trop. Med. Hyg., **19**, pp. 420–454.

Cooling, L. E. (1924). The larval stages and biology of the commoner species of Australian mosquitoes with the biology of *Aëdes pecuniosus* Edwards. —Serv. Publ. Dep. Hlth Aust. trop. Div., no. 8, 40 pp.

Edwards, F. W. (1922). Mosquito notes. III.—Bull. ent. Res., **13,** pp. 75–102.

Laird, M. (1946). A report on material obtained during a mosquito survey at Palmalmal, New Britain, July–October, 1945.—Trans. roy. Soc. N.Z., **75,** pp. 465–478.

Laird, M. (1954). *Anopheles* and malaria at Aneityum, New Hebrides.—Bull. ent. Res., **45,** pp. 279–283.

Muirhead Thomson, R. C. (1951). Mosquito behaviour in relation to malaria transmission and control in the tropics.—219 pp. London, Arnold.

Mumford, E. P. (1942). Mosquitoes, malaria and the war in the Pacific.—Science, **96,** pp. 191–194.

Perry, W. J. (1946). Keys to the larval and adult mosquitoes of Espiritu Santo (New Hebrides) with notes on their bionomics.—Pan-Pacif. Ent., **22,** pp. 9–18.

Perry, W. J. (1950). The mosquitoes and mosquito-borne diseases on New Caledonia, an historic account: 1885–1946.—Amer. J. trop. Med., **30,** pp. 103–114.

Puri, I. M. (1949). Anophelines of the Oriental Region.—*In* Boyd, M. F. *Ed.* Malariology, **1,** pp. 483–505. Philadelphia, Pa., Saunders.

Theobald, F. V. (1913). Culicidae from New Caledonia and the Loyalty Islands. —*In* Sarasin, F. & Roux, J. Nova Caledonia. Zoologie, **1,** pp. 161–164.

Williams, F. X. (1943). Mosquitoes and some other noxious flies that occur in New Caledonia.—Hawaii. Plant. Rec., **47,** pp. 205–222.

Note.—The name *Culex pipiens fatigans* Wied. is adopted in this paper in preference to *Culex fatigans* Wied., the name by which this form has hitherto been known. The authority for this change is to be found in Mattingly and others (Trans. R. ent. Soc. Lond., **102,** pp. 331–382, 1951 (R.A.E., (B) **40,** pp. 62–67)).—Ed.

EXPERIMENTS IN THE USE OF INSECTICIDES FOR THE PROTECTION OF GRAIN IN STORAGE.

By R. Le Pelley and S. Kockum.

Department of Agriculture, Kenya.

The control of insects in stored grain has always occupied attention, but special interest in this subject has been aroused in recent years by the realisation of the importance of lessening the very great losses of food which occur through insect infestation after the grain is harvested. In summarising the proceedings of the International Meeting on the Infestation of Foodstuffs, of the Food and Agricultural Organisation of the United Nations in London, August 1947, the Chairman, Mr. W. McAuley Gracie, said " it is absolutely established that there is a problem of great magnitude, deserving and demanding prompt attention and it is better to save food that has already been grown at great expense of labour and material than to develop large additional acreage to offset the wastage caused by infestation."

Amongst the papers dealing with East African work on this subject the following may be mentioned. Harris (1938) published results of some trials of various dusts on stored sorghum; the losses in eleven months were, untreated 23 per cent., wood ash 1 in 30, 17 per cent. and lime 1 in 50, 12 per cent. Darling (1947), after experiments with various dusts to protect maize in storage, concluded that kaolin and eucalyptus wood ash may give a degree of protection from attack for 2 or 3 months, and phosphatic dusts could give effective control for at least six months. Beckley (1948) reported that pyrethrum treatments of wheat against *Calandra oryzae* (L.), using fairly finely ground pyrethrum powder at the rate of 1 lb. per bag, gave " excellent to complete protection for eight and a half months, a most unexpected life." Apart from this, however, there appeared to be little certain information in Kenya on the value of different insecticides nor how they work in practice. It was decided in 1948, therefore, that experiments should be started to ascertain what insecticides were of value and to find the answer to some of the problems involved in their use, and a series of experiments was begun, the results of some of which are now available.

In the meantime the results of some further East African work on this problem have become available which are summarised here. Harris (1950) using a 0·5 per cent. γ BHC dust on seed maize found 91 per cent. of grains damaged, with a germination of 28 per cent. in the untreated control bags after 6 months, while in bags treated with 2 oz. of the dust (*i.e.*, about 3 parts per million γ BHC) 1 per cent. of the grains were damaged, with a germination of 68 per cent. Swaine (1952) found that excellent control of *C. oryzae* was achieved in millets and sorghum by admixing BHC at the rate of 0·5 parts of γ BHC per million of grain with the top and bottom layers of grain in silos. *Tribolium castaneum* (Hbst.) was not controlled at this dosage. Michelmore (1952) using heavy doses of diatomite, namely 1 to 100 lb. of maize at 14 per cent. moisture content, found 100 per cent. of the grains infested in two untreated bags after 9 months, with only 5 per cent. and 2 per cent. of grains infested in two treated bags after a year.

The first two experiments herein described were preliminary in nature (although one was on a very large scale) and they themselves posed some difficult questions which are partly answered by later experiments. The method followed in this paper is to give in sufficient detail the conditions of the experiments and the results obtained, set out after statistical analysis, and then to give some deductions from the analysis. It is hoped, however, that the layout of the information is such that anyone may draw his own conclusions from it.

The work was begun by one of us (R. Le P.), who planned and supervised Experiments I and II to their conclusion. Experiment III was in progress when the other (S. K.) joined the work. Since that time all experiments, though planned and prepared for publication jointly, have been carried out mainly by S. K., who has also done the statistical computation. Statistical analysis and reports were made by Mr. P. Robinson of the East African Agriculture and Forestry Research Organisation.

Experimental Work.

General methods used.

The usual method of carrying out experiments on the protection of grain in storage is to make laboratory studies in jars or very small bags with detailed counts and to extend this to large full-scale storage trials where general observations rather than detailed counts form the basis for assessment of results.

A particular feature of the experiments here described is that they were carried out in full-sized bags in normal storage premises. It was hoped that they might give direct results which would not require further confirmation before application in practice. We may consider shortly how far this was achieved. The experimental methods were not wholly effective because when the conditions approximated to normal storage practice (in the earlier experiments) the uncontrolled factors are considered to have prevented reproducible results; whereas when sufficient of the disturbing factors were controlled the experiment had become more in the nature of a laboratory trial with less of the direct relation to normal storage conditions which was desired. The first objection to experiments on bag scale of the size of those described is the great labour involved, where months of work are occupied by the sample counting, and this is a difficulty which normally cannot be overcome. The later experiments, however, while approximating to laboratory trials, nevertheless retained the valuable feature that they were carried out in the bulk of grain (namely the 200 lb. bag) used in storage. To apply the results to storage practice with bag stacks it is only necessary to consider differences arising from effects of bulking the bags into stacks, such as exposure of top and sides of the stack, distance of bags from the ground, heating of the insides of stacks, and similar phenomena; and the difficult considerations of how far the results in jars or small bags can be related to the 200 lb. bag are eliminated. Too often, we believe, the results of experiments in jars are considered to indicate what will happen in storage, without any study of the relationship of insect multiplication in such very small bulks to that in the standard 200 lb. bag.

As a result of the series of experiments described in this paper the following points emerge as important when setting up experiments of this type:

1. Insecticides must be carefully mixed in among the grain; the use of pressure probes is not permissible since the dosage they apply is not uniformly distributed.
2. The stacking must be very carefully considered, since there are exposed-end, side and top effects, and also effects of different distances from the ground. This can be allowed for in the statistical interpretation if adequate replication is available, but in the later experiments the bags were placed on the ground all separately spaced not touching any other bag, which gives much more consistent results.
3. Moisture content of grain is of importance chiefly through its influence

on the breeding of *C. oryzae*, but its influence on the physical condition of the dust may have some importance also.

4. The sampling must be uniform, and a long probe, sampling the whole length of the bag, should be used.

Counting of insects was confined to adults owing to the large number of samples entailed in these trials. Time did not permit of insects being bred out from samples. Further work is planned to improve the experimental methods still further. The carbon dioxide production method (Howe & Oxley, 1944) to estimate the larvae present will be used, though it may not be practically possible to determine for all the large number of samples necessary. Experiments are planned to compare the results obtained in jars and in full sized bags, to determine to what extent the results in jars are reproducible in bags.

Experiment I.

Object.—To test the effectiveness against *Calandra oryzae* of treatments of BHC, DDT, and pyrethrum each in two diluents, a local bentonitic clay and a local diatomite, also the diluents separately, and untreated grain as control.

Method.—Five randomised blocks each of 12 treatments (including two forms of pyrethrum and controls in duplicate) using full-sized 200 lb. maize sacks. The sacks were placed well separated in the randomised positions. In the space available they were placed upright and supported by ropes to prevent any bag touching another. The treatments were:

	Bentonite	Diatomite
BHC	A	B
DDT	C	D
Pyrethrum powder	E	F
Pyrethrum extract	G	H
Inert dusts only	I	J
Untreated controls ...	K	L

The BHC was a fine powder concentrate known as "Agrocide 7" and stated to contain 2·6 per cent. of the γ isomer. This was mixed into each of the diluents to give a dose of 0·5 parts of γ BHC per million parts of grain when 8 oz. of the mixed dust was added to a 200 lb. bag of grain. The DDT used (stated to contain 84 per cent. of the p,p′compound) was carefully and intimately mixed with the diluents so as to give a dose of 7 parts technical DDT per million of grain with 8 oz. of the mixed dust to a bag. The pyrethrum powder (pyrethrin I, 0·66 per cent.; pyrethrin II, 0·53 per cent.; total pyrethrins, 1·19 per cent.) was mixed with each of the diluents at the rate of $\frac{1}{2}$ lb. of powder to $\frac{1}{2}$ lb. of diluent and 1 lb. of the mixed dust was used to a bag, thus giving a dose of about 30 parts of total pyrethrins per million of grain. The pyrethrum extract (containing pyrethrin I, 16·24 per cent.; pyrethrin II, 11·94 per cent.; total pyrethrins, 28·18 per cent.) was taken up in petroleum ether and sprayed on to the diluents and intimately mixed for several hours. The concentration of pyrethrins in each of the diluents was 0·25 per cent., and 8 oz. of each diluent was added to a 200 lb. bag giving a dose of 6·25 parts of pyrethrins per million of grain.

Sieving analysis showed that 100 per cent. of the bentonite passed the Institute of Mining and Metallurgy Standard * (IMM) 240 mesh sieve and 99·96 per cent. passed the 300 mesh sieve. What is here called bentonite is a local type of bentonitic clay described by Pulfrey (1947) as follows. "The better quality [local bentonitic] clays are soapy when moist and swell to about three times their original volume when wetted. Research . . . suggests that the clays are composed predominantly of nontronite and illite."

---

* These standard sieves are 8 in. diameter with the diameter of wire and lineal aperture of mesh equal. The screening area of the screens is standard throughout the range, *viz.* 25 per cent. The size of the aperture, being half the mesh number expressed as a fraction of an inch, a No. 240 mesh has 1/480 in. aperture.

With diatomite 99·6 per cent. passed the 200 mesh sieve, 99·5 per cent. the 240 mesh and 99·0 per cent. passed the 300 mesh. The diatomite is described in Bull. imp. Inst. (Anon., 1945). It is a lacustrine diatomite composed predominantly of species of *Melasira*. When powdered it has a more fine-grained and generally more even-grained nature than many diatomites. The pyrethrum powder was the local standard fine ground powder, reground once through the finest sieve available. In the final sieving analysis the percentages passing the 50, 60, 80, 100, 120, 160, 200, 240 and 300 mesh respectively were 96·8, 83·7, 61·2, 54·4, 48·7, 27·7, 23·6, 18·2 and 13·3. The diluents when used alone were added at the rate of 8 oz. to a 200 lb. bag.

Application to the grain was made on 17th June 1948, the mixing being done with shovels on tarpaulins.

Sampling.—Samples were taken from each bag at monthly intervals and the dead and live insects in the samples were recorded. Sound and damaged grains were separated and weighed. The samples were mixed samples taken with a small probe at top, middle and bottom levels from two sides of the bag.

Results.—The weight of damaged grain was calculated as a percentage of the total weight, and these percentage weights are used in Table I which gives the treatment means from July 1948 to February 1949.

TABLE I.

Percentage damaged grain by weight, in Experiment I.

Sampling date	A	B	C	D	E	F	G	H	I	J	KL	L.S.D.	
												1	2
16th June 1948	16·0	16·7	14·6	17·2	17·6	15·0	15·2	15·7	16·6	16·7	17·1		
2nd July ..	16·0	17·7	17·0	14·1	15·0	16·1	18·9	17·4	19·4	16·9	15·7	3·30	3·81
16th July ..	14·5	19·0	16·9	15·2	14·8	15·6	19·7	18·2	17·7	14·9	15·3	4·38	5·06
30th July ..	18·8	18·6	20·3	19·2	16·2	18·2	22·1	22·2	22·2	18·4	17·4	5·46	6·31
13th Aug. ..	19·3	25·1	21·7	21·9	20·2	22·7	26·4	25·6	25·5	19·9	18·3	5·41	6·26
27th Aug. ..	20·0	24·5	24·1	20·8	19·1	21·6	27·9	25·5	25·7	22·3	18·0	5·26	6·07
24th Sept. ..	21·1	27·6	26·7	21·0	20·8	23·1	29·0	26·8	27·5	25·3	21·7	5·63	6·49
25th Oct. ..	20·8	22·2	25·3	21·5	25·7	24·0	36·6	25·7	33·3	20·7	27·8	6·90	7·97
25th Nov. ..	22·0	27·0	29·8	22·7	29·9	25·8	44·9	27·4	38·6	24·5	28·5	6·73	7·77
29th Dec. ..	20·7	24·6	26·6	21·8	27·7	23·0	46·3	29·4	39·4	23·4	31·4	7·05	8·13
26th Jan. 1949	22·1	25·5	29·3	23·1	34·4	24·4	49·6	28·7	43·2	20·7	30·0	7·58	8·77
23rd Feb. ..	21·9	26·1	28·0	22·7	43·4	24·2	55·3	27·1	57·8	22·7	32·0	6·88	7·95
23rd Feb. adjusted	22·1	25·9	29·0	22·2	42·3	25·0	56·1	27·5	57·5	22·7	31·5	6·35	7·34

L.S.D.: The last two columns give the least significant difference between treatment means: (1) is for comparison of any treatment with the control and (2) for a comparison between any two other treatments. For key to the letters see page 297.

For the statistical analysis the percentages were transformed into degrees by the use of Table XII in the " Statistical Tables " of Fisher and Yates (1948). The last two columns give the differences which are significant at the 5 per cent. level of probability, between means of treated and untreated bags (1) and between the means of treated bags (2). These differences are referred to as least significant differences (L.S.D.). They were calculated using the transformed figures in the formula for Student's t-test, and were then reconverted to percentages which are given in the Table. This can be done without serious error for the means of treatments, as they lie in a region where the scale of conversion is approximately linear. The last line of the Table is adjusted for lack of uniformity at the start, by the analysis of co-variance, from figures obtained on 16th June 1948. Some deductions, relative to the conditions of the experiment, which seem justified from the analysis may be listed:—

Diatomite alone (J) has a protectant effect, it was significantly better than the control in the last three samplings.

Bentonite (I) alone has not a protectant effect. On the contrary, it was significantly worse than the control from August onwards.

Pyrethrum powder in bentonite (E) and pyrethrum extract in bentonite (G), at the strengths used have not a protectant effect. The former was significantly worse than the control at the last sampling, the latter at all samplings after August. The pyrethrum extract (G) had no effect, and the pyrethrum powder (E) little effect in reducing the "tonic" effect of the bentonite (I) over the full term of the experiment.

Pyrethrum powder in diatomite (F) was significantly better than the control but not significantly different from diatomite alone (H).

BHC in bentonite (A) was significantly better than the control from December onwards, but in diatomite (B) though better than the control at all samplings this did not at any date reach significance.

DDT in bentonite (C) was significantly better than bentonite alone (I) but not significantly better than the control. DDT in diatomite (D) was not significantly better than diatomite alone (J), but both were significantly better than the control. At the last sampling date approximately 8 months from the start, four treatments were significantly better than control, namely BHC in bentonite (A), DDT in diatomite (D), pyrethrum in diatomite (F) and diatomite alone (J).

None of these can be considered notably effective from a practical point of view, and the experiment indicates that the dosage of insecticides (which, in the case of DDT and BHC were chosen as being the maximum at that time allowed by the authorities) may have been too low for adequate weevil control. Later experiments proved that this was the case with DDT and BHC but not with pyrethrum, but it is not known why the pyrethrum powder was not completely effective in this experiment.

Experiment II.

Object.—To test the effectiveness against *C. oryzae* of treatments of DDT, BHC and pyrethrum in all possible combinations, diluted with a local bentonitic clay and a local diatomite.

Method.—There were available bags of grain that were clean and very little infested, having passed through a conditioning plant (cleaning, heating and drying), and other bags of fresh grain untreated at the time of the experiment which were appreciably insect infested. There were eight treatments with each diluent and each was used in 10 bags of conditioned and 10 bags of unconditioned grain, a total of 320 bags. The toxicant in each case was diluted with one ounce of diluent, the treatments were:

(A)	1 oz. diluent only.
(B)	BHC 0·5 parts of γ BHC per million of grain.
(D)	DDT, 7 parts of DDT per million of grain.
(P)	Pyrethrum powder, 17·5 parts of total pyrethrins per million of grain.
(BD)	BHC and DDT together, each at above rates.
(BP)	BHC and pyrethrum powder together, each at above rates.
(DP)	DDT and pyrethrum powder together, each at above rates.
(BDP)	BHC, DDT and pyrethrum powder, the three together at above rates.

The bentonite and diatomite were very fine powders of which a sieving analysis has been given in Experiment I. The pyrethrum powder, kindly provided by the Pyrethrum Board of Kenya, contained 1·40 per cent. total pyrethrins and had the following sieving analysis. The percentages retained on IMM standard screens of 70, 100, 150, 200 mesh were respectively 2, 11, 52 and 10 per cent. whilst 25 per cent. passed through a 200 mesh. The application was made with a bag probe which had apertures for injection of the dust into bags, using a petrol-driven air compressor, each measured dose being separately placed in the powder container of the injector. The bags after injection were stacked horizontally eight high in randomised blocks with 10 replications of each treatment. Only a small amount of diluent was used because it takes a considerable time to force dust through the probe into the bag. At least the finest fraction of each dust percolated through the whole of the grain mass since it was seen to " smoke " out of all exposed sides of the bag. Examination of bags similarly treated afterwards showed that the deposit was not even, being many times heavier near the probe than away from it. This fact invalidates the bag probe method of application of an insecticide whenever the permitted dose is approximately equal to the effective dose, since in order to be effective at the periphery it would be necessary to overdose heavily at the site of the probe.

Sampling.—Every bag was sampled three times, namely before the application of the poisons, after four months and after eight months, which was the full term of the experiment. Sampling was made with a small probe from the end of the horizontally placed bags. The dead and live insects in the samples were recorded, and sound and insect-damaged grains were separated and recorded.

Results.—The percentage damaged grain and the calculated least significant differences (5 per cent. level) at the 8-month period adjusted for lack of uniformity at the start are given in Table II. The data were transformed into degrees as in Experiment I for statistical analysis, and the means reconverted to percentages. The means of 40 and 80 bags lie on that part of the scale where the transformation is approximately linear and there is, therefore, no serious error involved in reconverting the L.S.D. into percentages. With means of 10 bags the range is from about 10 per cent. to 40 per cent., and in the lower part of this range, from about 10 per cent. to 16 per cent., the figure for the L.S.D. is an overestimate.

TABLE II.

Percentage damaged grain by count (means of 10 bags).

	A	B	D	P	BD	BP	DP	BDP	Mean
W ..	46·5	28·0	30·9	29·3	19·5	23·8	24·7	24·1	28·1
X ..	37·5	32·3	32·5	28·4	35·7	27·4	22·6	24·8	30·0
Y ..	22·0	9·9	22·8	21·4	17·7	16·1	18·2	16·6	17·9
Z ..	17·0	12·9	23·1	13·6	14·6	17·7	21·1	15·7	16·8
Mean ..	30·1	19·8	27·1	22·8	21·4	21·0	21·6	20·1	22·9

Least significant differences (10) 8·7
" " " (40) 4·3
" " " (80) 3·5

Key to letters in Table:— W—Bentonite, unconditioned grain; X—Diatomite, unconditioned grain; Y—Bentonite, conditioned grain; Z—Diatomite, conditioned grain. Other letters as already given on page 299.

The Table shows that there was no overall difference between bentonite and diatomite in their effect on the percentage of damaged grain. As this is not in accordance with the findings of the first experiment we conclude that it is because both diluents were applied below the effective dose. The most outstanding difference is that between conditioned and unconditioned grain. Whereas at the start of the experiment in November the conditioned grain had far more grains damaged than the unconditioned grain, the percentage of damaged grain at the end of the experiment showed the reverse to be true; in other words the unconditioned grain suffered far more than the conditioned grain during the course of the experiment. The explanation of this fact is clear. The infested grain was passed through the conditioning process because it was heavily infested; this gets rid of the infesting insects almost completely, and consequently this grain started the experiment with a great advantage over the unconditioned grain. This unconditioned grain measured by count of damaged grains appeared at the start to be less infested but it then contained a population of living insects in all stages. The comparisons therefore between single treatments in conditioned and unconditioned grain are not really valid since in the former the insecticides had to act chiefly as protectants against insects entering from outside and in the latter they had to act to prevent increase of insect infestation already well established. The experiment makes it clear that the conditioning process itself is of great advantage in protecting grain over a long period as is shown by the significant differences when comparing the 80 bags with bentonite in each of two conditions of grain and similarly the 80 with diatomite in each of the two conditions of grain. It is known from other experimental work, however, that the conditioning process, as carried out in the grain dryer and conditioner used, does not completely destroy all insect life.

Considering the overall effect of each treatment (in 40 bags) BHC is significantly superior to diluents and DDT, but not to pyrethrum or combinations; pyrethrum is significantly superior to diluents only; the results give an indication that it is superior to DDT but this does not quite reach the level of significance. DDT is not significantly different from diluents or pyrethrum and is significantly less good than all the rest. All the combination treatments are significantly superior to diluents and to DDT, but not significantly superior to BHC or to pyrethrum.

Turning to the results from 10 bags in each treatment it is shown that in the unconditioned grain with bentonite all treatments without exception are significantly superior to bentonite alone. This together with the findings of Experiment I may be considered to dispose of bentonite by itself as a protectant. In the conditioned grain (which shows a much lower infestation) the only treatment significantly superior to bentonite is BHC, and in the other treatments there appears to be a detrimental interaction between BHC and other insecticides since in almost every case the combination treatments are significantly worse than BHC alone. In the case of unconditioned grain with diatomite, three of the combination treatments only are significantly superior to the diatomite alone. In the conditioned grain with diatomite there is no significant result with any treatment.

The experiment shows mainly negative results (which is unfortunate in view of its size and the labour involved), for example, it is clear that the method of application of the insecticides is quite unsatisfactory since it does not result in even distribution through the bag. It shows that the diluents alone did not prevent or induce a marked increase in infestation, but it must be borne in mind that in this experiment they were used at a very low dosage, lower than would ordinarily be used in practice. As regards the insecticides, the results are mainly negative also. Since there is an appreciable though not adequate result with BHC and with pyrethrum this suggests that these insecticides might be valuable at a greater dosage. DDT is not shown to be effective, and if effective at all, is clearly here at far too low a dose. Beneficial effect was not achieved by combining the insecticides except in one case where BHC and DDT together were significantly better than DDT alone.

Experiment III.

Object.—To test the effectiveness against *C. oryzae* of treatments of pyrethrum powder, pyrethrum powder with diatomite, and diatomite, using untreated grain as control.

Method.—A randomised block layout using a total of 48 bags giving 12 bags of each treatment arranged in three blocks of 4 layers with one treatment in each layer of each block. The treatments were:

(A) Local diatomite, 1 lb. per bag.
(B) Untreated controls.
(C) Mixture of pyrethrum powder (25 per cent.) and diatomite (75 per cent.), 1 lb. per bag.
(D) Pyrethrum powder (0·98 per cent. total pyrethrins), 4 oz. per bag.

The dusts were mixed with the maize by sprinkling them on the grain as it went through the hopper of an automatic grain weighing machine. A very small loss of dust occurred as seepage through the bags, this was collected from paper spread under one bag of each treatment and weighed, giving diatomite 5·4 gm.; pyrethrum-diatomite mixture 2·7 gm.; pyrethrum powder 1·9 gm. The maize was not specially mixed at the start, because it was from a single bulk and it was considered that any initial differences in damage would be accounted for in the statistical treatment of the results. Unfumigated maize was used and the experiment was set up on 23rd February 1950 and carried on till 12th January 1951.

Sampling.—Samples were taken, at intervals of about 6 weeks, from the end of the bags with a short sample spear and counts were made of damaged and undamaged grains and weights of each category were recorded. Numbers of live and dead insects and species were recorded from each sample.

Results.—The percentage of damaged grain at 14th November 1950 corrected for variation at the start on 6th March 1950 is given in Table III.

TABLE III.

Percentage damaged grain by count (means of 4 bags), 14th Nov. 1950.

	Treatments				
	A	B	C	D	Mean
Layers 1 ..	24·0	41·2	21·7	53·0	35·0
2 ..	27·3	34·6	25·7	28·4	29·0
3 ..	23·8	41·7	23·8	32·6	30·5
4 ..	30·3	47·5	28·0	35·5	35·3
Mean ..	26·3	41·3	24·8	37·1	

Least significant differences for body of Table: 13·7
" " " for means: .. .. 6·9

The four treatments are effectively divided into two pairs, pyrethrum-diatomite mixture and diatomite being better than pyrethrum and control.

There is little difference between the members of each pair. The bottom and top layers are worse than the two middle layers. The absence of protection with pyrethrum in this experiment no doubt results from the low pyrethrin content of the powder and the small dose, amounting to only 12·25 parts of pyrethrins per million of grain. Also, the important effect of hymenopterous parasites (later observed) was not considered in this experiment.

Experiment IV.

Object.—To test the effectiveness of (1) pyrethrum powder, (2) pyrethrum powder (25 per cent.) and diatomite (75 per cent.) mixture and (3) diatomite, in protecting insect-free maize from weevils, *C. oryzae*, present in a store.

Method.—A randomised block layout of 4 treatments (including control untreated) with 4 replications of each, a total of 16 bags. These were full-sized 200 lb. maize sacks lying flat on wooden dunnage with no bag touching another. Before treatment the maize was insect-free, having been fumigated with methyl bromide, and it was carefully mixed by repeated shovelling. The insecticides were carefully mixed in with a shovel, at the rate of 8 oz. per bag in each case. In previous experiments somewhat conflicting results had been achieved with pyrethrum, for example in the humid conditions of Beckley's experiments it gave good protection over a period of many months while in the dry conditions of some early experiments in this paper it was not superior to diatomite alone. For this reason it was decided to carry out this experiment at high humidity. The relative humidity of the store was maintained between 65 and 70 per cent. R.H. by means of a humidifier. Weevils were liberated into the store.

Sampling.—Monthly samplings were made from all bags using a long sampling spear which removed a sample throughout the whole length of the bag. Counts of damaged and sound grains were made on the samples taken at the start and the first four months thereafter and also on the last two samplings. Insect counts were made monthly throughout the course of the experiment.

TABLE IV.

Living *Calandra oryzae* per 100 kg. grain (means of 4 bags), in Experiment IV.

Date	Untreated	8 oz. pyrethrum	2 oz. pyrethrum 6 oz. diatomite	8 oz. diatomite
27th Nov. 1950	0	0	0	0
2nd Jan. 1951	132	0	0	0
2nd Feb.	100	0	20	21
2nd March	441	0	40	20
3rd April	3161	0	20	42
3rd May	9653	0	182	155
1st June	11031	181	1120	290
3rd July	69040	35	487	433
7th Aug.	35340	421	1544	751
4th Sept.	25046	811	2930	847
4th Oct.	21832	1805	4932	2848
5th Nov.	31652	6391	12704	17889
4th Dec.	58136	38502	63409	12010
7th Jan. 1952	33266	57971	27868	26580

Results.—The totals of living *C. oryzae* per 100 kilograms of grain (means of 4 bags) at all sampling dates throughout the experiment are given in Table IV. Percentages of damaged grain (means of 4 bags) at three dates are given in Table V. It is not considered necessary here to give the detailed figures of the statistical analysis carried out. Taking the counts of living insects there were no statistically significant differences in the first four and the last three months. Up to the 10th month there were significantly fewer *Calandra* in the pyrethrum bags than in the controls, and significantly fewer than in pyrethrum plus diatomite in the fifth, sixth and seventh months. In the sixth month the analysis showed that diatomite had significantly less living insects than the pyrethrum-diatomite mixture.

TABLE V.

Percentage damaged grain by numbers (means of 4 bags), in Experiment IV.

Date	Untreated	8 oz. Pyrethrum	2 oz. Pyrethrum 6 oz. Diatomite	8 oz. Diatomite
3rd April 1951 ..	8·61	3·55	3·71	4·11
4th Dec.	96·97	39·00	41·16	16·85
7th Jan. 1952 ..	97·35	71·34	60·56	41·05

Referring to the percentage of damaged grain (Table V) the amount of damage in the control bags became significantly greater than in all treatments by the fourth month (3rd April 1951). By the twelfth month (4th December 1951) damage had increased throughout but was markedly greater in the control than in all other treatments, but at this date both pyrethrum and pyrethrum with diatomite were significantly more damaged than diatomite alone.

From the sixth month onwards the parasite, *Anisopteromalus* (*Aplastomorpha*) *calandrae* (How.), was present in increasing numbers in the store room. Parasites were found in the samples from control bags as early as the sixth month. In the eleventh month they were first found in the samples from the bags with mixed pyrethrum and diatomite. Not until the thirteenth month were they present in the pyrethrum-treated grain. It seems clear that *A. calandrae* in undisturbed conditions can multiply sufficiently on a heavy infestation of *Calandra* to reduce the population of living adults. The presence of pyrethrum, on the other hand, may, by its effect on parasitism, act so as to favour the increase of *Calandra*. This could happen, though it has not been proved, if pyrethrum is still active against the parasite when it has deteriorated and lost its strength against *Calandra*. This would allow the weevils to increase and to reach numbers higher than in untreated maize. It is clear that the effect of inert dusts and insecticides is not a simple reaction of weevils to these substances, but the reaction of a complex population of beetles and their parasites and this will have to be considered in evaluating the results of experiments.

Pyrethrum powder (1·45 per cent. total pyrethrins) at the rate of 8 oz. per 200 lb. bag of grain under the conditions described, controlled weevils completely for more than five months and kept down the numbers considerably for ten months. The dosage in this case amounts to 36 parts of pyrethrins per million of grain, and this is above the dosage, 25 p.p.m., for which official approval has been given. Pyrethrum 2 oz. plus diatomite 6 oz. was not better than 8 oz. of diatomite alone but after six months it showed signs of being worse, which is confirmed by counts of damaged grain during the last two months of the experiment. For storage of more than ten months diatomite alone proved the best protectant.

Experiment V.

Object.—To test the effectiveness against *C. oryzae* of treatments of pyrethrum powder, pyrethrum and synergists, BHC and various diluents.

Method.—A randomised block giving five replications of each of eight treatments. The maize was fumigated with methyl bromide to render it insect-free. All the grain was taken out of bags and thoroughly mixed by repeated shovelling. The treatments were applied by dusting the insecticide into the stream of grain passing through the hopper of an automatic Avery weighing machine into new bags. The bags were placed in a randomised block lying on wooden dunnage with no bag touching another. The treatments were:

(A) Proprietary grain protectant stated to consist of a special grade of fibrous talc impregnated with piperonyl butoxide and pyrethrins, giving an active ingredient content of 0·8 per cent. piperonyl butoxide and 0·05 per cent. pyrethrins, used at the rate of 6 oz. to 200 lb. of grain.

(B) Grain protectant formulated locally for the experiment consisting of a finely ground local soapstone impregnated with piperonyl butoxide and pyrethrins giving an active ingredient content of 0·8 per cent. piperonyl butoxide and 0·05 per cent. pyrethrins used at the rate of 6 oz. to 200 lb. of grain.

(C) Diatomite 8 oz. to 200 lb. grain.

(D) Pyrethrum powder (1·30 per cent. pyrethrins) finely ground, 6 oz. to 200 lb. of grain.

(E) 0·04 per cent. γ BHC in diatomite, 8 oz. to 200 lb. grain.

(F) Control—untreated.

(G) Grain protectant partly proprietary and partly formulated locally, giving an active ingredient content of 0·8 per cent. piperonyl butoxide and 0·05 per cent. pyrethrins, made up of constituents (1) and (2) below, the mixture of these used at the rate of 6 oz. to 200 lb. of grain.

    (1) Proprietary grain protectant concentrate (same make as (A) above) stated to consist of a special grade of fibrous talc impregnated with piperonyl butoxide and pyrethrins, giving an active ingredient content of 4 per cent. piperonyl butoxide and 0·25 per cent. pyrethrins: 1 part.

    (2) Finely ground local soapstone: 4 parts.

(H) Finely ground local soapstone (from the Kisii District, Kenya) 4·8 oz. to 200 lb. grain.

Sampling.—Sampling was carried out with a long probing spear, reaching through the whole length of the bag, three probes being taken for each sample. From the weighed samples, counts were made of the different insect species found alive and dead. After removing the insects, the samples were fumigated (to prevent breeding during the period of the counts) and counts were made of sound and damaged grains, number and weight being recorded. Insect counts were made at monthly intervals from March when the experiment was started, and grain counts (which occupy a great deal of time) made at the start and after 6, 9, 11, 12, 15, 16, 17 and 18 months. One bag had to be discarded as porcupines had got into the store and eaten most of its contents and a value for this missing bag was calculated for each sampling by the method given by Davies (1947). The store contained large amounts of infested grain.

Results.—The insects found in the samples included *C. oryzae*, *Gnathocerus cornutus* (F.), *Tribolium castaneum*, *Rhizopertha dominica* (F.), *Oryzaephilus surinamensis* (L.), *Tenebroides mauritanicus* (L.), *Laemophloeus* sp., *Carpophilus* sp., *Sitotroga cerealella* (Ol.), other Lepidoptera and some Rhynchota and Hymenoptera. Of these only *Calandra* and *Gnathocerus* were present in large numbers.

The populations of these two species are shown in figs. 1 and 2.

The adult *Calandra* population in the untreated bags increased fast during the first months but, before the population had reached a density sufficiently high to cause a decrease through overcrowding, the parasite, *Anisopteromalus calandrae*, began to make itself felt and this quickly reduced the population and finally controlled it around a comparatively low average. There is reason to believe that the oscillations shown in the figures may be oscillations above and below a mean density typical of the enemy/prey (or parasite/host) interaction, in accordance with mathematical theory (Volterra, 1931). The physical environment in this case was constant enough to allow an approximation to the theoretical expectation in a case of simple uncomplicated interaction. In maize treated with finely ground soapstone the insect encounters a difficulty because of the slippery nature of the ground soapstone. The population did not rise so high as in untreated grain and was later controlled by the parasite at about the same level as in untreated grain. The soapstone used has been described by Pulfrey (1946) and consists mainly of sericite and kaolinite. In the diatomite-treated maize the effect is similar but because the material continues throughout to exert an effect through its slippery nature and probably a killing effect in addition, this appears to have kept the population down to a slightly lower level throughout. The pyrethrin-piperonyl butoxide mixtures gave way after six months and the *Calandra* population was thereafter controlled by parasites at about the same average density as in untreated maize. The pyrethrum treatment began to give way at nine months but had some effect up to about fourteen months. The dosage used was the officially approved limit of

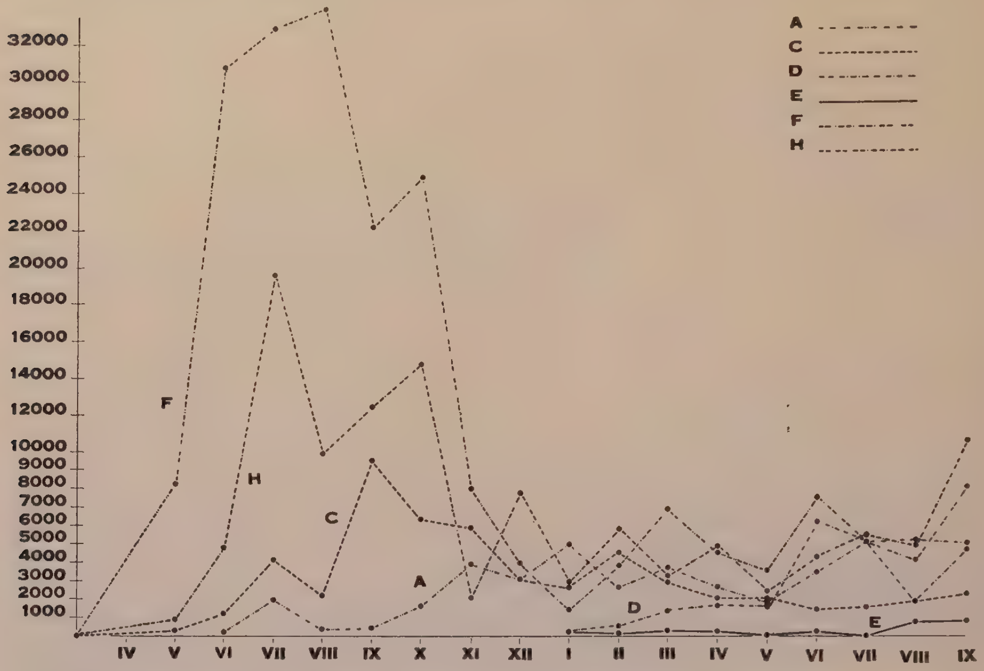


Fig. 1.—*Calandra oryzae*: adults alive per 100 kg. in Experiment V (mean of five samples). Data is not included where numbers are too low to allow clear reproduction. (A) pyrethrum-piperonyl butoxide; (C) diatomite; (D) pyrethrum powder; (E) BHC; (F) untreated; (H) soapstone.

25 parts of pyrethrins per million of grain. BHC at 1 part per million of γ BHC gave complete control for sixteen months and only then began to show a small rise.

Gnathocerus cornutus, a secondary pest mainly dependent for food on damage caused by *Calandra*, began to increase late in the experiment, reaching fairly high numbers in the untreated and soapstone-treated bags. When the insect was well established in these bags it spread to other treated bags where damaged grain was present. The fluctuations in populations suggest a parasite but this was not found. The percentages of living *Calandra* of the total numbers in the samples are given in fig. 3.

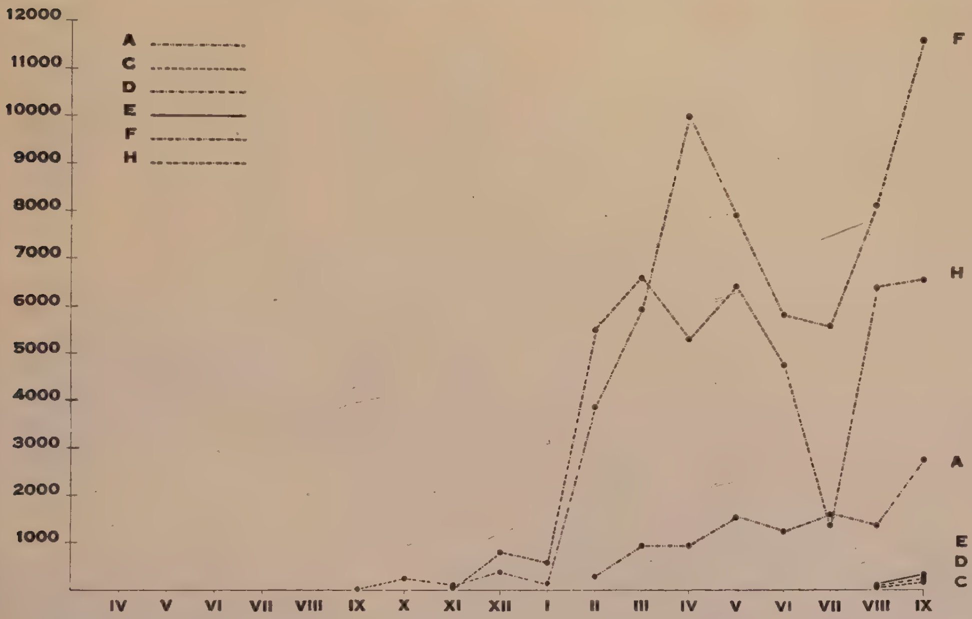


Fig. 2.—*Gnathocerus cornutus*: adults alive per 100 kg. in Experiment V (mean of five samples). Data is not included where numbers are too low to allow clear reproduction. (A) pyrethrum-piperonyl butoxide; (C) diatomite; (D) pyrethrum powder; (E) BHC; (F) untreated; (H) soapstone.

This figure shows that a majority of the insects in the controls, in diatomite and in soapstone treatments are living insects, whereas in all other treatments soon after the start the majority of insects are dead. The breakdown of toxicity is also indicated at about the eighth month for the pyrethrin-piperonyl butoxide mixtures, about the eleventh month for pyrethrum, while in the BHC, though there are some minor fluctuations (perhaps not significant), approximately 90 per cent. of the insects are dead in the samples taken throughout the whole of the eighteen months of the experiment.

It has previously been taken that the chief beneficial effect of diatomite is due to the fact that it kills weevils. This is not borne out by the results of this experiment, and the tentative conclusion is drawn that its effect is mainly due to its slippery nature which prevents the easy distribution of insects through the bulk. It is hoped to test this possibility experimentally later.

The counts of sound and damaged grain expressed as percentages of damaged grain by number gave the results shown in Table VI. The analysis in this case was made direct without converting to degrees.

The results agree well with what could be expected from the occurrence of live insects from month to month as illustrated in fig. 1.

The insecticides used in this experiment were effective for different times—1 p.p.m. γ BHC for more than 15 months, pyrethrum for more than 9 months, pyrethrin-piperonyl butoxide mixtures for 6 months, diatomite, after an initial rise, steady up to 18 months at a low level of damage and soapstone little or no protective effect but populations lower than in untreated maize.

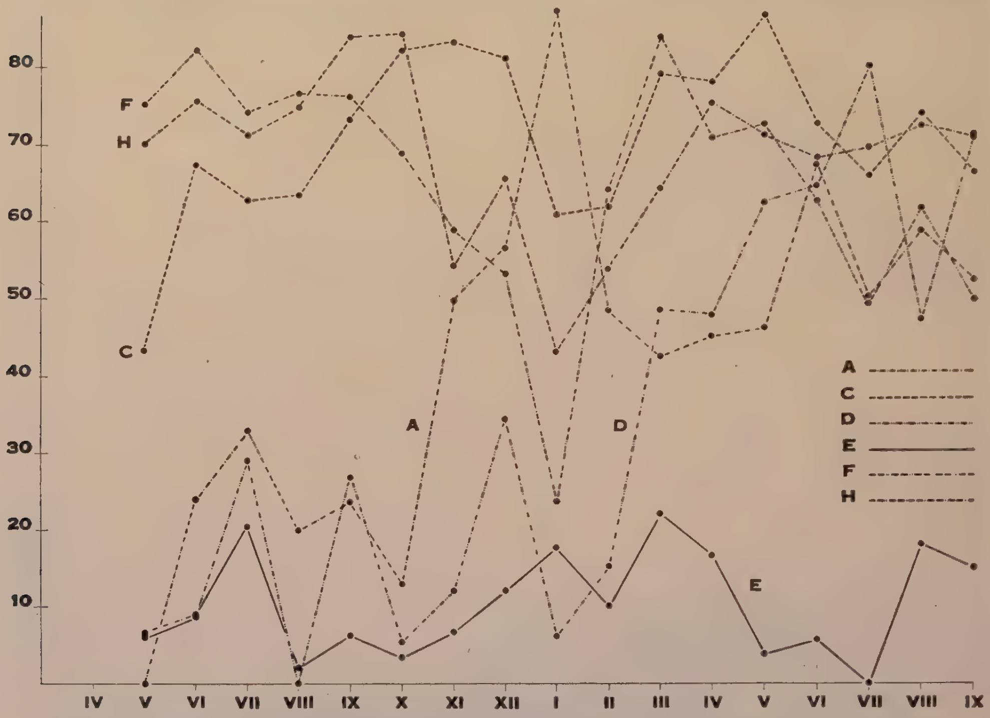


Fig. 3.—*Calandra oryzae*, percentage alive of total present in Experiment V. (A) pyrethrum-piperonyl butoxide; (C) diatomite; (D) pyrethrum powder; (E) BHC; (F) untreated; (H) soapstone.

TABLE VI.

Percentage of damaged grain by count (means of 5 bags).

Months from beginning of expt.	Index letters of treatments								
	A	B	C	D	E	F	G	H	L.S.D.
6	6·19	6·25	9·01	4·08	6·09	70·38	6·00	23·51	6·91
9	24·04	28·55	17·13	3·63	5·76	62·06	17·67	54·99	16·99
12	18·23	19·82	15·66	5·24	6·26	69·80	19·55	61·57	11·99
15	24·42	24·88	19·61	16·38	5·62	80·38	34·55	62·09	12·15
16	25·00	24·80	19·12	20·07	6·05	79·09	35·69	66·27	13·71
17	30·84	33·06	18·12	19·38	11·06	79·69	31·37	62·90	12·93
18	45·10	49·79	20·81	38·19	17·23	83·64	46·33	68·82	17·51

Average initial damage 7·2 per cent.

Pyrethrum Powder as a Grain Protectant.

Beckley's results (1948) with pyrethrum powder against *C. oryzae* have already been quoted. The pyrethrin content of the powder he used is not given but it may be assumed to have been at least 1 per cent. total pyrethrins, and his dosage was therefore not less than 50 parts per million of grain. In the same paper he indicates that 8 oz. of powder (25 parts per million) would be sufficient. These results are substantiated by Parkin (1951) (though working with a different insect species and over a shorter period) who states "Laboratory tests have shown that wheat may be adequately protected at 25°C. against infestation by *Calandra granaria* by uniform admixture of 0·25 per cent. or more by weight of a pyrethrum powder containing 0·97 per cent. w/w total pyrethrins." This is approximately 24 parts per million. Howe (1952) used pyrethrum powder in bagged groundnuts and reported "half a pound per bag can be recommended as a dosage rate. The average reduction in losses suggested by these experiments is about 1·5 per cent. of the tonnage of treated nuts." He also used pyrethrum powder at different rates in bagged cocoa beans against *Lasioderma serricorne* (F.) in southern Nigeria where humidity is high and reported that downgrading occurred in all bags, the treated deteriorating to the greatest extent.

Pyrethrum was used in a number of different experiments here described and though the results were not entirely consistent, they merit a general word. From consideration of the results at the range of dosages employed it is possible to judge with fair certainty the dosage required for effective use. For example, the lowest dosage using a pyrethrum extract (Expt. I) namely 6·25 parts of pyrethrins per million of grain was completely ineffective, the next, 12·25 p.p.m. (Expt. III), was not significantly effective, a dosage of 17·5 p.p.m. (Expt. II) proved to have some effect and was significantly better than the inert diluents. At 25 p.p.m. (Expt. V) it was completely effective by insect counts for 8 months and according to percentage of damaged grain for 12 months. At 36 p.p.m. (Expt. IV) it was also highly effective. The indications are that the officially approved limit of 25 p.p.m. is about the minimum for really effective use. Experiment IV was carried out at a high humidity but it is not proved that this has an important influence on its effectiveness. Parasites undoubtedly affect the results of experiments with pyrethrum and this factor has not been fully studied.

Summary.

Five experiments in the use of insecticides against *Calandra oryzae* (L.) in stored maize are described. The results with statistical analysis and deductions are given. The insecticides used were BHC, DDT, pyrethrum, pyrethrin-piperonyl butoxide mixtures; the diluting dusts used were a local diatomite, a local bentonitic clay, and a local soapstone.

Among the chief conclusions are the following:—

The insect damage in conditioned grain did not reach, throughout an eight-month period, the high level which it did in unconditioned grain, the conditioning process alone therefore is a valuable treatment for insect control.

Bentonite alone is not a protectant and its addition to grain may on the contrary provide a more favourable environment for *Calandra*.

A Kenya soapstone (from Kisii) is not an effective protectant but had some effect in reducing *Calandra* populations over the period when an initial increase was occurring in control bags.

Kenya diatomite is a protectant. It reduces the percentage of grain damaged, but when used in bagged grain this is not proved to be due solely to intrinsic toxicity, but may in fact be due chiefly to the slippery nature of the material inhibiting insect distribution through the bulk of grain.

Gamma BHC at 1 p.p.m. is completely effective for 16 months.

Gamma BHC at 0·5 p.p.m. has some protectant effect but is not fully effective.

DDT at 7 p.p.m. has not a protectant effect.

Pyrethrin-piperonyl butoxide mixtures were effective for 6 months. The content of active insecticide used was too low for effective weevil control over a long period.

Pyrethrum powder, using 6 oz. or over to a bag, to give a pyrethrin content of 25 parts per million of grain or over, is a good protectant, having given good protection up to 10 months.

Anisopteromalus calandrae (How.) has an important influence on the infestation of *Calandra* and must be considered in experiments. In the last experiment it brought the *Calandra* population down in untreated bags and the population was then maintained with minor fluctuations, about a mean of low population.

Acknowledgements.

We owe acknowledgement to a large number of people for assistance with these experiments. To a former assistant, Mr. I. Cormack, for his careful sampling and moisture determinations in Experiment I. To Mr. R. G. Smith, for help with sampling in other experiments and much other general help. To Dr. H. C. Pereira for help in designing the statistical layout especially for Experiment II. To Mr. P. Robinson, East African Agriculture and Forestry Research Organisation, for statistical advice and reports at all later stages of the work. To Col. R. C. Swain, Controller, Maize and Produce Controls, for his interest and for facilities for experimentation. To Mr. G. L. Laing, then of "Atlantic Products", for applying insecticides and other help. To the Pyrethrum Board of Kenya, and A.E. & C.I. Limited for supplying insecticides and for their interest and help. Finally, to several African laboratory assistants for their careful work in the examination of samples.

References.

ANON. (1945). Recent analyses and tests of a Kenya diàtomite.—Bull. imp. Inst., **43**, pp. 55–58.

BECKLEY, V. A. (1948). Protection of grain against weevils.—E. Afr. agric. J., **14**, pp. 71–76.

DARLING, H. S. (1947). Report of the Entomologist.—Rep. Dep. Agric. Uganda, 1945–46, pt. 2 pp. 16–30.

DAVIES, O. L. (1947). Statistical methods in research and production.—p. 116. Edinburgh, Oliver & Boyd.

FISHER, R. A. & YATES, F. (1948). Statistical tables for biological, agricultural and medical research.—3rd edn., p. 56. Edinburgh, Oliver & Boyd.

HARRIS, W. V. (1938). Annual report of the Entomologist for the year 1937.—Ent. Leafl. Dep. Agric. Tanganyika, no. 16, 8 pp.

HARRIS, W. V. (1950). Report of the Senior Entomologist.—Rep. Dep. Agric. Uganda, 1947–48, pt. 2 pp. 1–5.

HOWE, R. W. (1952). Experiments on the use of pyrethrum powder as an admixed dust in the tropics.—Pyrethrum Post, **2**, no. 4 pp. 4–6.

HOWE, R. W. & OXLEY, T. A. (1944). The use of carbon dioxide production as a measure of infestation of grain by insects.—Bull. ent. Res., **35**, pp. 11–22.

Michelmore, A. P. G. (1952). Section of Entomology. General progress report. —Rec. Invest. Dep. Agric. Uganda, 1949–50, pp. 4–22.

Parkin, E. A. (1951). A laboratory test of pyrethrum powder to protect grain against infestation by weevil.—Pyrethrum Post, **2,** no. 3 pp. 11–14.

Pulfrey, W. (1946). The nature and origin of soapstone from near Kisii.—J. E. Afr. nat. Hist. Soc., **19,** p. 51.

Pulfrey, W. (1947). The geology and mineral resources of Kenya.—Bull. imp. Inst., **45,** pp. 277–299.

Swaine, G. (1952). 1950 Annual report of the Entomologist, Morogoro.—Rep. Dep. Agric. Tanganyika, 1950, pp. 175–178.

Volterra, V. (1931). Variations and fluctuations of the number of individuals in animal species living together.—*In* Chapman, R.N. Animal ecology, pp. 409–448. New York, McGraw-Hill.

REARING *DROSOPHILA MELANOGASTER* MG. FOR INSECTICIDE INVESTIGATIONS.*

By R. W. Kerr.

Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Plate XXIX.)

In rearing *Drosophila melanogaster* Mg. as a test species for insecticide investigations certain factors should be taken into account to ensure as much uniformity as possible in the batches of test flies. The susceptibility of the adult flies to insecticides has been shown to vary with their age (Morrison, 1943; McLeod, 1944; Kerr, 1954). The number of larvae developing in a given amount of food is of some importance, since overcrowding delays development, extends the period of adult emergence (Sang, 1949), and reduces the size of the adult flies produced (Stultz, 1940; Sang, 1949). It has also been indicated by Stultz that the age of the parent flies, at the time new cultures are set up, may influence the susceptibility of the resulting test flies. Obviously these factors require standardisation, and this can best be achieved by starting each culture with a standard number of eggs laid in the shortest possible time by females of standard age.

The rearing method of Hodson and Chiang (1948) was examined in some detail, as it appeared to be the only one described which provided a means of collecting eggs at regular intervals, and of using known numbers of them to set up new cultures. Several generations of Rothamsted wild-type flies were reared, but, due largely to a different egg-laying habit in this strain of flies, the method proved less successful than Hodson and Chiang found with their flies. The apparatus involved was rather unstable and not easily transportable, and the cultures required far more attention than could conveniently be given.

The methods generally employed in genetical laboratories for maintaining stocks of this species, and those described by Stultz (1940), Caldwell (1949) and Bartlett (1951) for large-scale rearing, are all much simpler in the design of the apparatus used and require little attention to the cultures during the developmental period. However, in all of these methods, cultures are started by allowing females to lay unknown numbers of eggs directly on to the culture medium, so that the degree of standardisation desirable in rearing test flies is not achieved. Any one of these methods could be easily modified to allow for such standardisation, thereby increasing its efficiency in rearing test flies.

The following rearing procedure was based on a typical maintenance method. It took into account all of the factors discussed above, and was found to give a very uniform production of flies, so that the approximate numbers maturing to the desired age on the test days could be predicted.

The Rearing Method.

Adults and oviposition.

Newly emerged flies were transferred from the larval cultures to half-pint milk bottles bearing a muslin or parachute-nylon sleeve attached with cellulose tape and closed with a rubber band. The bottles were stored horizontally on light wooden racks ($18\frac{1}{2}$ in. × 6 in. × 7 in. high) holding two rows of six bottles (see Pl. XXIX, fig. 1). To conserve bench space in the rearing room, the racks were constructed so that they could be placed one above the other and linked together at each end with hooks and screw-eyes. A detachable metal handle was hooked into the screw-eyes of the top rack.

---

* This work was carried out while the writer was stationed, during 1951, with the Department of Insecticides and Fungicides, Rothamsted Experimental Station, Harpenden, Herts, England.

Food and water containers for these bottles were made from corks, and 2 in. × $\frac{3}{4}$ in. specimen tubes, respectively. The corks were excavated with a $\frac{1}{4}$ in. cork-borer to a depth of $\frac{1}{4}$ in., and were then water-proofed by immersing in melted paraffin wax. The "wells" in the waxed corks were filled with the food described by Hodson and Chiang. This food consisted of equal parts of honey and compressed bakers' yeast which, when mixed, formed a syrup thin enough to prevent the flies from ovipositing in it. The tubes were filled with water and wet cotton-wool plugs inserted, care being taken to exclude air bubbles. Over the surface of each plug was placed a circle of black filter paper $\frac{3}{4}$ in. in diameter. The water tubes and food corks were held together with galvanised iron wire clips, thus forming a compact unit which could be easily handled with crucible tongs when being inserted into, or removed from, the bottles containing adult flies. A wire clip and completely assembled unit are shown in Plate XXIX, fig. 2. Approximately 300 flies could be accommodated in each bottle without overcrowding. The food and water units were changed every 24 hours.

The water tubes were included to provide convenient moist oviposition surfaces, but when it was found that eggs were also laid on the waxed corks, tests were conducted to determine whether the water tubes were really necessary. At relative humidities of 40–50 per cent. in the rearing room, and with daily changes of food, flies died within 48 hours when water tubes were not supplied, but survived for at least 14 days when the humidity in the bottles was increased by the inclusion of water tubes. Under the latter conditions, flies survived equally well whether they could drink from the water tubes or not.

Eggs.

Oviposition commenced when the flies were 4 days old, the eggs being laid exclusively on the surface of the waxed cork surrounding the food "well" and on the filter paper circle in the water tube. Clusters of eggs can be seen in both of these situations in Plate XXIX, fig. 2. To avoid overcrowding in larval cultures, it was considered advisable not to exceed about 400 eggs per culture bottle. If sufficient eggs were not already present on the filter paper circle, more were added from the clusters laid on the food corks. The damp circles were then placed, egg-side downwards, on the surface of the medium in larval culture bottles.

Larvae and pupae.

The principal larval food was bakers' yeast growing on the standard medium used at Rothamsted, which was prepared in the following manner: 7·5 gm. of agar was boiled in 400 ml. of water until dissolved, and 0·25 gm. of Nipagin M* added; a solution of 15 ml. of treacle in 155 ml. of water was added to the agar solution, and 70 gm. of rolled oats stirred in gradually to avoid lumpiness. This mixture was cooked slowly with stirring for 40 minutes, and poured into half-pint milk bottles to a depth of about 1 in.

The bottles were stoppered with loose plugs of cotton wool, and when the contents had cooled, a few drops of an aqueous suspension of bakers' yeast, consisting of about equal parts of yeast and water were spread over the surface of the medium in each bottle. The culture bottles were then ready for the addition of eggs, after which they were stored in the rearing room maintained at a temperature of 24°C.

---

* A preservative for pharmaceutical preparations made by Nipa Laboratories, Ltd., London.

At this temperature the eggs hatched during the first day. The black filter paper circles, which bore the eggs, were removed on the second or third day to avoid discoloration of the medium. The larvae began to migrate up the sides of the bottle on the fourth or fifth day in search of pupation sites. Single sheets from pieces of cellulose wadding about 4 in. square were then loosely crumpled and placed in each bottle to provide a dry surface for pupation. Emergence of adults commenced on the ninth day, reaching a maximum on the eleventh or twelfth day.

During the emergence period the adult flies were transferred daily to oviposition bottles in which they were kept for egg-laying, or until required for experimental purposes. The age of the flies was thus known to within ± 12 hours. It was not known whether, in this strain, the age of the parent flies influenced the viability of the eggs they laid, or the susceptibility of their progeny to poisons. To guard against such possible sources of variability, experimental cultures were set up with eggs laid by females of a standard age, usually seven days.

Post-test conditions for adults.

The milk bottles with food and water units were entirely satisfactory for maintaining test flies *en masse* before insecticide tests. After treatment, the test groups were transferred to smaller and more convenient glass vials (3 in. × 1 in.) into the bottoms of which had been firmly pressed thin pads of absorbent cotton wool moistened with 3 ml. of aqueous food mixture. The vials were stoppered with loose plugs of cotton wool, and stored upright at 24°C. during the observation period.

Under these conditions the survival of untreated flies three days old, supplied with the various food materials listed in Table I, was determined experimentally. Each food treatment was tested with three batches of about 40 flies.

TABLE I.

Survival of flies on various foods.

Food treatment	Per cent. survival at x hrs.									
	24	48	65	72	89	113	137	144	161	168
Water only	96	29	0							
Yeast 5 per cent. in water ..	100	48	9	3	0					
Treacle 5 per cent. in water ..	100	100	100	100	99	97	79	67	8	0
Yeast 5 per cent. and treacle 5 per cent. in water ..	100	80	10	5	1	0				
Yeast 5 per cent. and treacle 5 per cent. in water (vials on their sides)	100	98	52	35	6	0				

Judged on nutritional grounds alone, yeast + treacle in water should have been a highly satisfactory food, and the poor survival of flies was attributed to the effect of the carbon dioxide generated by the actively growing yeast. When the vials containing this mixture were stored on their sides to allow the carbon dioxide to diffuse out through the cotton wool plugs, survival was slightly better. The effect of carbon dioxide on this strain of flies is discussed elsewhere (Kerr, 1954).

The treacle and water mixture was outstandingly the best food, and kept the flies alive for at least three days. Mortality after three days was due to desiccation accompanying the observed drying out of the food pads. In all subsequent experiments with insecticides the flies were supplied with treacle and water after testing.

Summary.

A method is described for rearing *Drosophila melanogaster* Mg., which provides a high and consistent yield of adult flies, of uniform age and size, for insecticide studies.

Acknowledgements.

I wish to thank Dr. F. Tattersfield, Miss J. Kerridge and Mrs. L. R. Taylor, of the Insecticide Department, Rothamsted Experimental Station, for freely giving me the benefit of their experience in the use of *Drosophila* as a test insect. Mr. P. H. Needham, of the same Department, kindly photographed the apparatus used.

References.

Bartlett, B. R. (1951). J. econ. Ent., **44**, p. 621.

Caldwell, A. H. (1949). J. econ. Ent., **42**, p. 707.

Hodson, A. C. & Chiang, H. C. (1948). Science, **107**, pp. 176–177.

Kerr, R. W. (1954). Bull. ent. Res., **45**, pp. 323–328.

McLeod, W. S. (1944). Canad. J. Res., (D) **22**, pp. 87–104.

Morrison, F. O. (1943). Canad. J. Res., (D) **21**, pp. 35–75.

Sang, J. H. (1949). Physiol. Zoöl., **22**, pp. 183–202.

Stultz, H. T. (1940). 70th Rep. ent. Soc. Ont., **1939**, pp. 72–80.

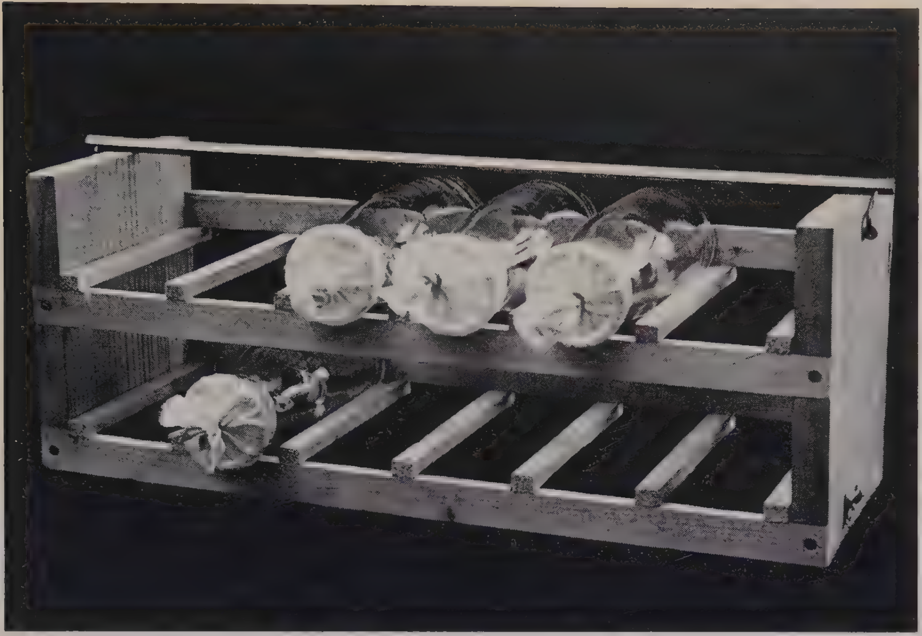


FIG. 1. A wooden rack holding the bottles used for accommodating adult flies during oviposition or prior to testing.

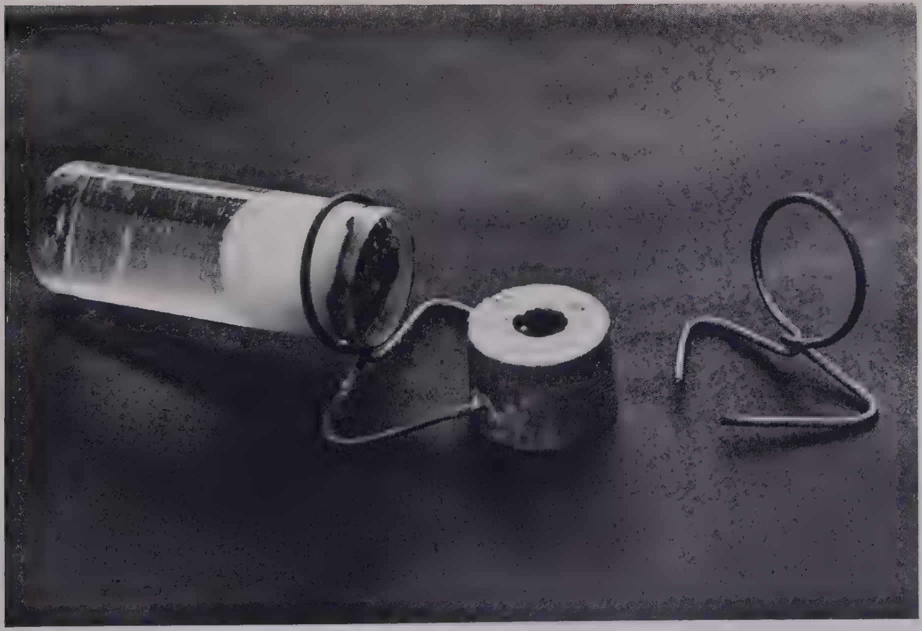


FIG. 2. A food and water unit after removal from an oviposition bottle and a spare wire clip which holds the water tube and food cork together. Masses of eggs are visible on the top surface of the waxed cork and the black filter paper circle in the mouth of the water tube.

A METHOD FOR THE TOPICAL APPLICATION OF SMALL MEASURED DOSES OF INSECTICIDE SOLUTIONS TO INDIVIDUAL INSECTS.*

By R. W. Kerr.

Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Plates XXX & XXXI.)

For the topical application of measured doses of insecticides to insects, various types of apparatus have been described. Some of these have been reviewed by Richardson (1943). Calibrated micropipettes of glass capillary tubing were used by Nelson and others (1934) and by Stafford (1946) for dispensing single doses. The microburette has been widely favoured since several doses can be dispensed to one filling, and the magnitude of the dose can be altered to compensate for variations between individual insects, such as in body weight or surface area.

The simplest type of microburette, described by Worthley (1943), consisted of a straight capillary tube with a tapered tip bent at a right angle. The dose was measured against a linear scale which was read with the unaided eye. For accuracy in dosing, Worthley suggested that the bore of the tubing should be such that the required dose occupied 5–10 mm. of the capillary. In the similar burette of Woodbury and Barnhart (1939) smaller doses were rendered possible by using finer tubing (thermometer capillary) and a lens to read the dosage scale. Obviously the requirements of speed in dosing, and the number of doses dispensed to one filling of burettes of this type, limit the extent to which the bore can be reduced, and hence place a lower limit on the dose which can be accurately dispensed.

McGovran and others (1940) and Scholander (1942) designed microburettes of greater sensitivity which involved the use of a micrometer screw plunger and an intermediary liquid to expel the dose. These were of necessity considerably more elaborate in design.

A microburette, with a greatly increased range and accuracy, but which preserved the simplicity of Worthley's design, was described by Kerr (1948, 1951). Like Worthley's, the burette itself consisted of an open-ended piece of capillary tubing drawn at one end to a tip bent at a right angle. The increase in accuracy was achieved by using a microscope to view the capillary. A 1-cm. eyepiece micrometer with 100 divisions served as the scale for measuring the doses, and its image being superimposed on that of the capillary, parallax errors were thus reduced to a minimum.

As a result of the magnification employed, it was not necessary to use tubing of extremely small bore for the burette. Hence it could be made to hold considerably more doses than would otherwise have been possible. The bore, being comparatively large, offered little resistance to the flow of most of the liquids used on to insects held against the tip, and additional pressure to speed up delivery was only necessary with liquids of high viscosity.†

---

* This work was carried out while the writer was stationed, during 1951, with the Department of Insecticides and Fungicides, Rothamsted Experimental Station, Harpenden, Herts, England.

† The most suitable liquids were those of low volatility and viscosity which spread rapidly on the waxy surface of the insect cuticle.

One of the main advantages of this instrument was that, by employing various combinations of objectives and eyepieces, several overlapping ranges of doses could be covered by any one burette, without greatly altering the accuracy in dispensing. Furthermore, the small size of the doses which could be dispensed made possible the use, as solvent-carriers for the insecticides, of liquids which in larger doses would be toxic themselves. A disadvantage was that the insect being dosed and the image of the capillary and scale were not in the same field of vision. This was not found to be a necessity in dosing insects the size of house-flies, but smaller insects required closer and more frequent inspection to ensure that the doses were applied to the correct position on the body. The disadvantage was overcome in the present apparatus which has the same basic form but greater sensitivity. It was developed to apply doses of the order of 0·01 μl. to flies of the species *Drosophila melanogaster* Mg., and its use for this purpose is described here.

Description of the Method.

Microburette.

The microburette for dispensing insecticide solutions was made in the following manner from a 6-in. length of precision-bore glass capillary tubing with external diameter 6 mm. and bore 0·2 mm. The tubing was sealed at one end by fusion and the bore near the heated end was expanded to about 3 mm. After cooling, it was then reheated by a small-jet flame directed at the region where the bore commenced to expand. The tubing was rapidly drawn at this point. The drawn portion was bent at a right angle to the rest of the tubing and cut at a convenient point to form a tip which was then progressively shortened until the required flow-rate was obtained. The tip was sealed with paraffin wax, ground flat, and smoothed on carborundum stones and a leather strop. The wax prevented occlusion of the capillary by carborundum and glass fragments, and was easily removed by ether. The external and internal diameters of the finished tip were 0·22 and 0·03 mm. To the free end of the burette was attached a short length of rubber tubing with a glass mouth-piece to facilitate filling and cleaning.

The burette was mounted horizontally, in spring clips, on the mechanical stage of a microscope, with its tip directed downwards. It was filled, by suction, from a vial of insecticide solution, to a point at which the meniscus in the capillary was in the field of the microscope. The solution remained stationary in the burette, but flowed out at a convenient rate when wettable objects were held against the tip. By means of a prism, mirror, and convex lens, the image of the meniscus, together with that of a micrometer scale mounted in the eyepiece, were projected on to a small white screen mounted on the mechanical stage close to the tip of the burette. The screen was shielded from extraneous light from the microscope lamp, and the tip of the burette was locally illuminated by a narrow beam of light from a shielded pea-lamp also mounted on the mechanical stage. The assembled apparatus is shown in Plate XXXI, fig. 1. Plate XXX, fig. 1, shows the microburette clipped on to part of the mechanical stage which also carries the white screen to the left, and the pea-lamp housing behind the tip of the burette.

By setting up the apparatus in a darkened room and localising the light required in handling the insects, a clear projected image of the meniscus and scale was obtained with a standard 30-watt microscope lamp.

Operation of microburette.

Odourless distillate was chosen as the most suitable solvent for the insecticides on the basis of its viscosity, volatility, and low toxicity to the flies. Both males and females can tolerate volumes of at least 0·03 μl. applied to the mesonotum. As the solvent flowed out of the burette on to the mesonotum of the fly held against the tip, the image of the meniscus moved along that of the scale at a steady rate. The flow stopped immediately the fly was removed, so that any required volume could be dispensed simply by removing the fly quickly at the appropriate time. The image of the meniscus was reset to the reference point by turning the knob which moved the mechanical stage. Thus a considerable number of measured volumes could be delivered without refilling the burette.

With the microscope eyepiece and objective used, the complete scale of 100 divisions represented a volume of 0·035 μl. After some practice, the volume delivered could be controlled to within one scale division, so that the error involved was less than $\frac{100}{n}$ per cent., where n = the number of scale divisions applied. If the required volume was inadvertently over-shot by more than one scale division, the treated fly was discarded. The volumes usually employed were 0·01 μl. (29 divisions) for males, and 0·016 μl. (46 divisions) for females, the errors thus being always less than 3·4 per cent.

Handling of flies during treatment.

The flies were kept in half-pint milk bottles before testing. To collect them singly and hold them sufficiently still during dosing, without the use of anaesthetics, the following technique was used. A glass filter funnel was fitted in the mouth of the bottle. It was held in place, inside the sleeve, by the rubber band normally used to close the sleeve. A collecting tube, consisting of a short length (7 cm.) of glass tubing, 2·5 mm. in bore, was plugged at one end with cotton-wool, and slipped into a "Perspex" adaptor fitted tightly on the end of the stem of the filter funnel (see Pl. XXX, fig. 2). The flies were disturbed by gently tapping the bottle, and migrated into the tubing towards a light placed in front of it. After 10–15 flies had passed into the tubing, it was quickly removed and plugged at the other end with cotton-wool, another collecting tube being inserted into the adaptor. The bore of the collecting tubes was just large enough to allow a fly to turn round, or two flies to pass each other, without difficulty. The flies were removed singly from these collecting tubes by means of the suction device shown in Plate XXX, fig. 3, which was made from a short piece of glass tubing, 2 mm. external diameter, cemented into a "Perspex" adaptor and connected by rubber tubing to a filter pump. At the free end where the fly was held, the bore had been reduced to a smooth-edged orifice about 0·38 mm. diameter by heating. In catching the flies with this device, suction was cut off by pinching the rubber tubing manually, the holder inserted into the collecting tube, which it fitted loosely, and the pressure released when an approaching fly was a few mm. from the orifice. The fly was sucked head-on on to the orifice and whilst thus held was removed from the collecting tube, sexed and treated. With the suction pressure reduced to the minimum required to hold the fly, handling by the above technique did not cause any injury.

After treatment the holder with the fly attached was inserted through a hole in a glass plate into an observation vial inverted over the hole. The fly was released by cutting off the suction, the holder withdrawn, and the vial slid over the plate away from the hole. Plate XXXI, fig. 2, shows two observation vials, one for flies of each sex, inverted over the glass plates. Immediately after treatment, each observation vial was stored at 24°C., and mortality counts were taken at suitable intervals, usually 24 and 48 hours later. Ten flies of each sex were generally used per treatment.

Discussion.

The smallest volume applied to *Drosophila* was 0·01 μl., and with a permissible dispensing error of 3–4 per cent., less than one-tenth of the flies had to be discarded because of overdosing. Experiments involving 100 flies were carried out conveniently in 2–3 hours, the time varying slightly according to the number of different treatments.

The microburette, as described, was capable of delivering, from one filling, a large number of doses within the range 0·005–0·035 μl., the percentage dispensing error being inversely proportional to the dose. For this range, the bore of the burette (0·2 mm.) and the magnifying power of the objective (10×) were neither excessively large nor small. It will be clear from the design of the apparatus that burettes of different bores and objectives of different powers could be readily substituted to cover additional dosage ranges, either higher or lower, without altering the rest of the projection system.

The accuracy in dispensing obviously depends on the velocity at which the image of the meniscus travels across the screen. Hence burettes for additional dosage ranges should be made with tips of suitable size so that this velocity is maintained within reasonable limits. As an alternative to changing the burette, one general purpose burette could be used, with different objectives, for a number of ranges, provided slight adjustments to the viscosity of the liquid are permissible.

Although designed for dosing *Drosophila melanogaster*, the apparatus and techniques could be readily adapted to suit other species of similar or larger size. The projection of the dosage scale into the same field of vision as the insect being dosed renders the microburette particularly suitable for dosing insects of small size, or for accurately applying small doses to selected parts of the bodies of larger insects.

Summary.

A microburette made from glass capillary tubing is mounted on the mechanical stage of a microscope and filled with insecticide solution to a point at which the meniscus is in the field of the microscope. The magnified images of the meniscus and a calibrated micrometer scale in the eyepiece are projected on to a small screen mounted close to the tip of the microburette so that the scale and the insect being dosed can be seen simultaneously. This feature renders the apparatus particularly suitable for topical application work in which accurate positioning of the dose on the insect is required. When an insect, held in a suction device described, is applied to the tip of the burette, the solution flows out unaided, and stops immediately the insect is removed. With the microburette described, doses from 0·005 to 0·035 μl. can be dispensed to within ±0·00035 μl. The apparatus can be made to cover several other dosage ranges, either lower or higher, by simple modifications which are discussed.

Acknowledgements.

The help given by various members of the staff at Rothamsted is gratefully acknowledged. Messrs. A. J. Arnold and M. Elliott assisted in the construction of some of the apparatus, Drs. C. Potter and T. Goodey kindly loaned part of the optical equipment used, and Mr. P. H. Needham photographed the apparatus in its final form.

The photographs were prepared for reproduction by Messrs. L. A. Marshall and D. H. Wilson, C.S.I.R.O., Canberra.

References.

Kerr, R. W. (1948). Aust. J. sci. Res., (B) **1,** pp. 76–92.

Kerr, R. W. (1951). Bull. sci. industr. Res. Org. Aust., no. 261, 63 pp.

McGovran, E. R., Phillips, G. L. & Mayer, E. L. (1940). A measured drop method of applying liquid insecticides.—U.S. Dep. Agric. Bur. Ent., ET-165, 3 pp. multigraph.

Nelson, F. C., Buc, H. E., Sankowsky, N. A. & Jernakoff, M. A. (1934). Soap & sanit. Chem., **10,** no. 10, p. 85.

Richardson, C. H. (1943). Publ. Amer. Ass. Advanc. Sci., no. 20, pp. 126–135.

Scholander, P. F. (1942). Science, **95,** p. 177.

Stafford, E. M. (1946). J. econ. Ent., **39,** pp. 499–503.

Woodbury, E. N. & Barnhart, C. S. (1939). Soap & sanit. Chem., **15,** no. 9, pp. 93–113.

Worthley, H. N. (1943). Publ. Amer. Ass. Advanc. Sci., no. 20, pp. 140–143.

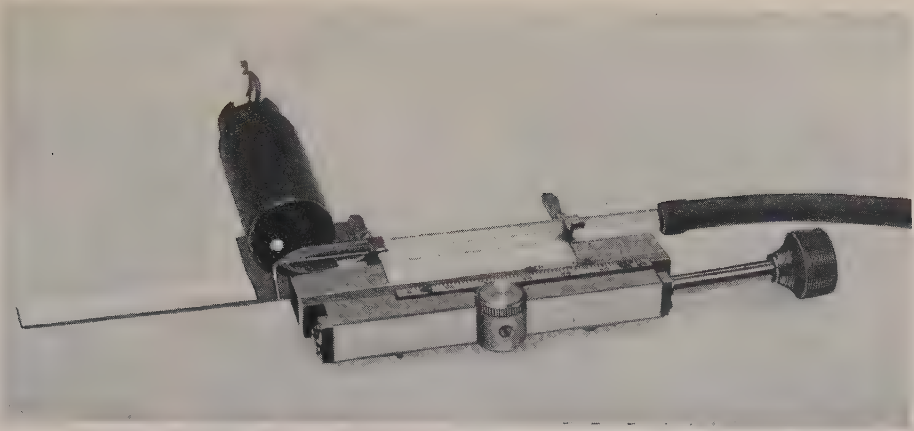


FIG. 1. Part of the mechanical stage showing the attachment of the microburette, lamp housing and white screen.

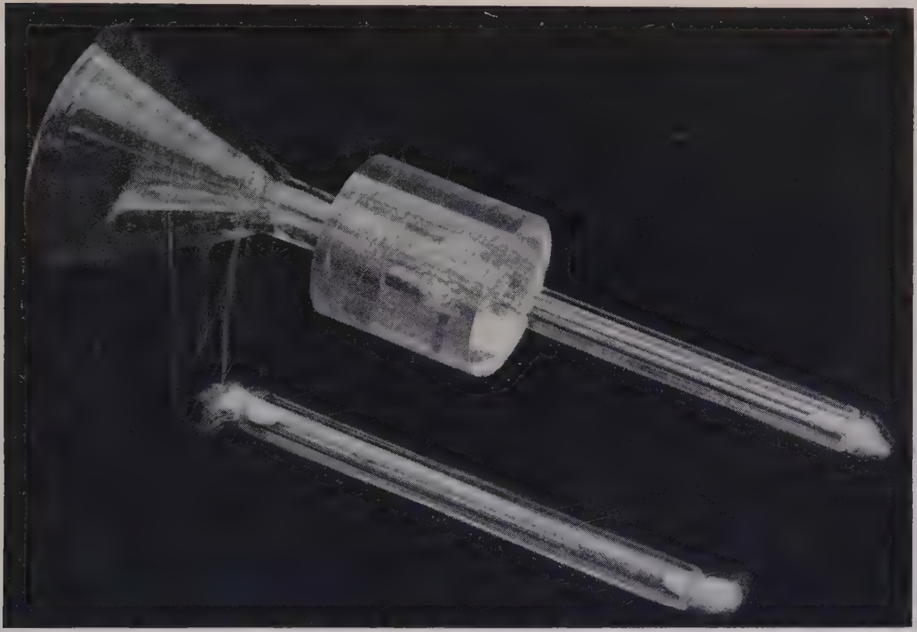


FIG. 2. Apparatus for collecting flies from the culture bottles. The glass funnel fits the neck of the bottle. Flies migrate through the funnel and "Perspex" adaptor into the removable glass collecting tube at the right, towards a light placed at this end of the apparatus. A spare collecting tube with cotton-wool plugs is shown below.

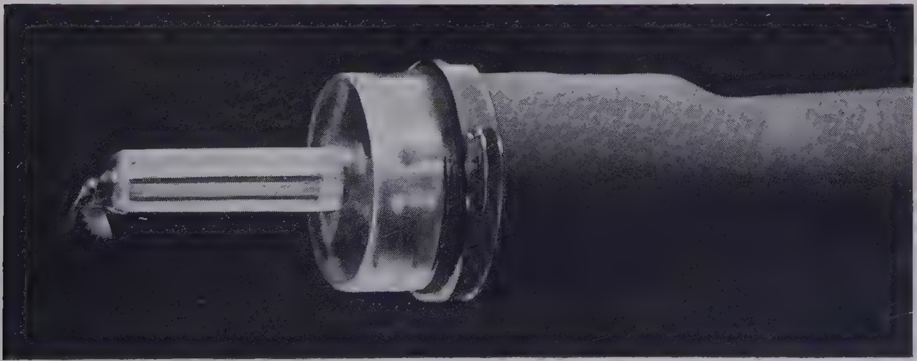


FIG. 3. Suction device for holding the fly by the head, as shown, while the insecticide is applied by bringing the mesonotum into contact with the tip of the microburette. The fly is caught by inserting the glass tube of the suction device into the collecting tube shown in fig. 2.

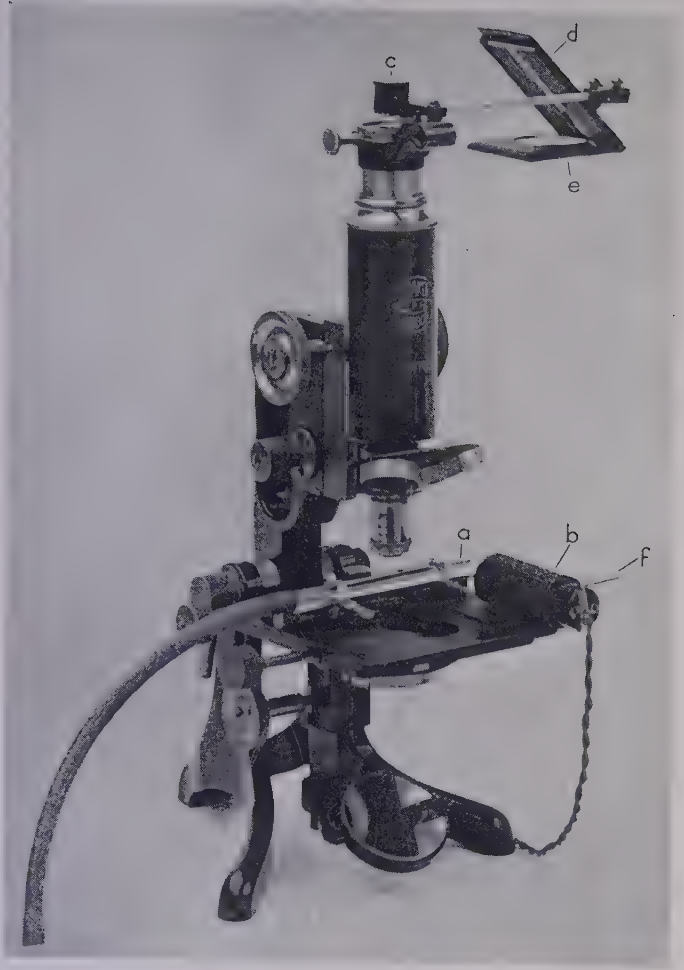


FIG. 1. Apparatus for dispensing measured doses of insecticide solution. showing the glass microburette (*a*) mounted on the mechanical stage of the microscope, and the housing (*b*) for the pea-lamp to illuminate the tip of the burette. The magnified images of the meniscus in the burette and the scale in the eyepiece of the microscope are projected *via* the prism (*c*), mirror (*d*) and lens (*e*) on to the white screen (*f*) near the tip of the burette.

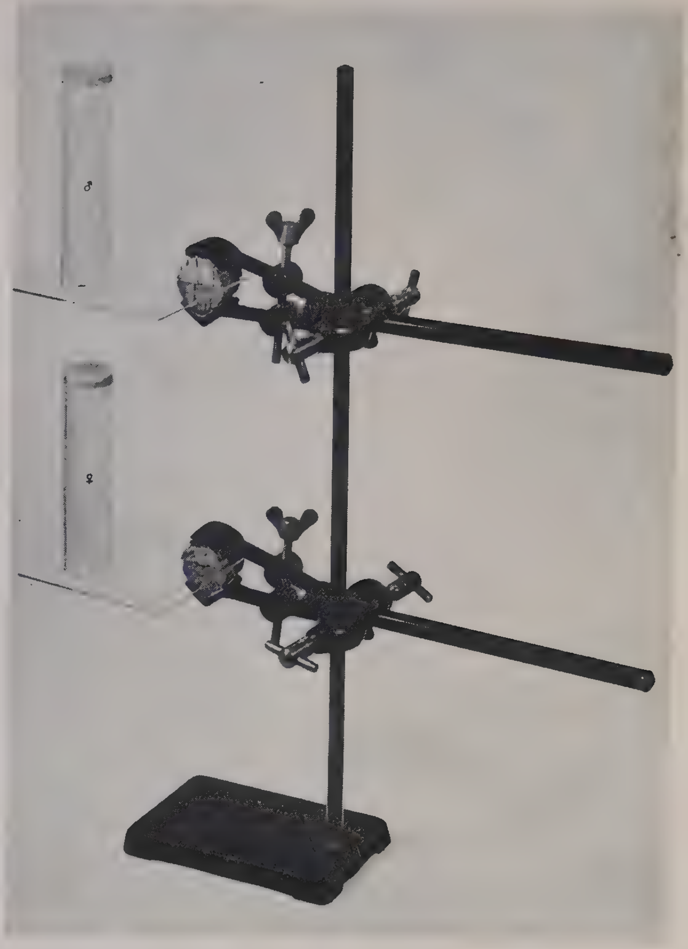


FIG. 2. Vials, containing food pads, inverted over holes in glass plates through which the flies are introduced after dosing.

VARIATION WITH AGE IN THE SUSCEPTIBILITY TO DDT AND THE RESPIRATION RATE OF MALE AND FEMALE *DROSOPHILA MELANOGASTER* MG.[1]

By R. W. Kerr.

Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

During a study of the development of resistance to DDT in *Drosophila melanogaster* Mg. currently being carried out at Rothamsted by Dr. F. Tattersfield, it became apparent that insufficient was known about the influence of sex and age of the adult flies on susceptibility to DDT. In the first attempts to evaluate these factors, by directly spraying groups of flies[2] of various ages with aqueous suspensions of DDT, using the apparatus designed by Potter (1941, 1952), the writer found it difficult to interpret the results, largely because of the unpredictable toxic effect of carbon dioxide which was used to anaesthetise the flies before spraying. A proportion of the flies failed to recover from the anaesthesia produced during short exposures to carbon dioxide, and this proportion was found to increase considerably with age of the flies. In some instances higher kills were obtained by spraying anaesthetised flies with the control spray (containing no DDT) than with sprays of low DDT concentration.

The treated flies in these preliminary experiments were kept at 24°C. during the observation period in upright vials stoppered with cotton-wool plugs and containing pads of absorbent cotton-wool moistened with a food liquid consisting of 5 per cent. of treacle and 5 per cent. of compressed bakers' yeast in water, as described elsewhere (Kerr, 1954*a*). It was suspected that the effect of carbon dioxide generated in the vials by the growing yeast also contributed to the high mortalities obtained in unsprayed controls.

For the purposes of this investigation, a method of applying DDT without previous anaesthetisation of the flies was needed. It might have been possible to use a spray technique to treat flies confined in wire screen cages, but under such conditions the variable behaviour of the flies during spraying and subsequent transference from the wet cages to clean containers would be expected to have influenced very markedly the dosages of spray accumulated and those actually retained by the individual flies after treatment. A high proportion of the spray would doubtless have accumulated on the fine mesh screen necessary to confine such small insects, and it would have been difficult to devise a method for transferring the sprayed flies to clean containers without contaminating the latter. It was obvious that the precision of the testing procedure would be greatly increased if the variable effect of fly behaviour on the dosage retained were eliminated by applying to individual flies constant doses which could not be removed subsequently. The advantages of controlling dosage in this way have been demonstrated with the house-fly (*Musca domestica* L.) (Kerr, 1951) 41 by using a microburette to apply small constant volumes of insecticide solutions to the mesonotum. A similar technique was therefore developed for treating *Drosophila*. Details of this technique and the method used for rearing the flies are given elsewhere (Kerr, 1954*a*, *b*).

---

[1] This work was carried out while the writer was stationed, during 1951, with the Department of Insecticides and Fungicides, Rothamsted Experimental Station, Harpenden, Herts, England.

[2] The flies used were from a laboratory colony, designated as Rothamsted wild type, which was started in 1948 with wild flies collected near Rothamsted. Prior to this investigation, the strain had been observed by Tattersfield to be sensitive to carbon dioxide. Only one instance of such sensitivity has been recorded, that of the ebony strain investigated by L'Héritier (1948) and his associates. The ebony strain was cultured at Rothamsted during 1942–1944 and was then removed. Whether the Rothamsted wild type derived its sensitivity, prior to collection, from crossing with escaped ebony flies, or developed it independently, is not known.

Susceptibility of five-day-old Flies to DDT.

The rearing, handling, and insecticide application methods referred to above were used in determining the susceptibility of five-day-old[3] males and females of the Rothamsted wild type flies to DDT. Five solutions of p,p′DDT in filtered odourless distillate, ranging in concentration from 0·2 to 0·4 per cent. w/v, were each applied in doses of 0·01 and 0·016μl. to the mesonota of ten males and ten females respectively. The test was repeated with flies from different cultures, and the solutions were applied in ascending and descending order of concentration alternately. Mortality counts were taken at 24 and 48 hours after treatment, but only rarely did flies die after the first 24 hours. Table I shows the mean 24-hour mortalities obtained.

TABLE I.

Mortality of five-day-old flies topically dosed with DDT solutions.

Dosage (μg. DDT/fly)		Per cent. mortality in 70 flies at 24 hours	
♂	♀	♂	♀
0·0400	0·0635	100	97
0·0336	0·0533	99	87
0·0283	0·0449	83	56
0·0238	0·0378	60	49
0·0200	0·0318	41	14

Probit analyses of the data, by the method of Finney (1947), showed homogeneity for both males and females, and the calculated equations for the regression of mortality in probits on log. dosage of DDT were:

$$Y = 1{\cdot}71 + (9{\cdot}73 \pm 1{\cdot}14)x \text{ for males,}$$
$$\text{and } Y = -0{\cdot}47 + (8{\cdot}99 \pm 1{\cdot}27)x \text{ for females,}$$
$$\text{where } Y = \text{mortality in probits, and } x = \text{log. dosage } (\mu\text{g.}) + 2.$$

From these equations the LD50 values for males and females were calculated to be 0·0218 and 0·0406 μg., or, on a body weight basis, 26·6 and 31·0 mg./kg. respectively. The χ^2 test showed that the departure of the regression lines from parallelism was not significant at the 5 per cent. level, so that the relative susceptibility of males and females could be expressed as the inverse ratio of the LD50 values, *i.e.*, 0·0406/0·0218 = 1·86. Taking body weight into account the relative susceptibility was 1·17.

---

[3] At the time of treatment the flies were actually 100–126 hours old, but for convenience their age was regarded as being 5 days.

Variation in Susceptibility with Age.

Using the same techniques, ten males and ten females from adult cultures 1, 3, 5, 7 and 9[4] days old were dosed with 0·01 µl. and 0·014 µl., respectively, of a 0·25 per cent. solution of p,p′DDT in filtered odourless distillate applied to their mesonota. The test was repeated twice with flies of the same ages, but from different cultures, and the order of treatment of the age groups was varied in the three tests. Mortality counts were taken at 24 hours after treatment. The results of these tests are given in Table II.

TABLE II.

Mortality of flies of various ages caused by a fixed dosage of DDT topically applied.

Sex	Age (days)	Dosage	Per cent. mortality at 24 hours			
			Test 1	Test 2	Test 3	Mean
♂	1	0·01 µl. of 0·25 per cent. DDT solution (= 0·025 µg. DDT)	80	90	100	90
	3		60	40	80	60
	5		40	20	40	33
	7		60	80	90	77
	9		90	70	100	87
♀	1	0·014 µl. of 0·25 per cent. DDT solution (=0·035 µg. DDT) ..	100	100	100	100
	3		20	30	10	20
	5		10	10	20	13
	7		20	20	30	23
	9		0	0	54·5*	18

* One extra fly treated.

Apart from one aberrant figure (marked with an asterisk) the results were fairly consistent. It is apparent that:

1. The susceptibility of males decreased with age up to five days, and then increased, up to nine days.
2. The susceptibility of females decreased rapidly during the first three days, and thereafter appeared to change little.
3. At three to nine days old, males were more susceptible than females.

In females there was a slight indication of a peak of "resistance" at five days, as in males, but the mortalities for three- to nine-day-old females were at too low a level for the recorded changes to have much significance.

Variation in Respiration Rate with Age.

Batches of about 50 adults of each sex and of ages 1, 3, 5, 7 and 9[4] days, were collected by a suction device and transferred to small glass vials, ½ in.

---

[4] At the time of treatment the flies were actually 4–30, 52–78, 100–126, 148–174, and 196–222 hours old, but for convenience their ages were regarded as being 1, 3, 5, 7, and 9 days.

diameter × $\frac{1}{2}$ in. high, covered with muslin. A small drop of honey was placed in the centre of each muslin cover. These vials of flies were placed in a series of Barcroft respirometers as modified by Dixon (1934, 1951) and described by Lord (1949). After equilibrium had been reached, as indicated by a steady oxygen uptake, records were taken of the volumes respired every 15 minutes for two hours. The means of these volumes, expressed as µl. per fly per hour are given in Table III.

TABLE III.

Respiration rate of untreated flies of various ages.

Age	Oxygen uptake (µl./fly/hour)	
	♂	♀
1	1·68	3·08
3	2·04	3·63
5	3·44	4·05
7	3·25	4·06
9	2·63	4·41

The respiration rate of males increased with age up to five days, and then decreased; that of females increased with age up to nine days. When the "resistance" to DDT of flies of these ages is expressed in terms of per cent. surviving the treatment, as in fig. 1, it will be seen that there is a positive correlation with respiration rate which is particularly close in the case of males.

Discussion.

The difference in susceptibility between males and females and the changes in susceptibility with age revealed in this investigation illustrate the desirability of sexing and standardising the age of flies used in toxicological experiments with DDT. In collecting groups of test flies from the cultures, the emergence period should be restricted as much as possible, for between groups there are bound to be slight differences in mean age due to variable rates of emergence. Taking both sexes into account, it appears from the curves in fig. 1 that such differences will have least effect on susceptibility when the flies are about five days old. In the interests of economy in rearing and uniformity in susceptibility, it is considered that the emergence period should not exceed 24 hours, and that the flies should be used for tests when their mean age is about five days.

The trends in susceptibility to DDT with age, recorded here, are similar to, but more pronounced than those found by Morrison (1943) in *D. melanogaster* adults sprayed with nicotine sulphate. Morrison's results indicate a minimum susceptibility in flies four days old (*cf.* five days for DDT), but he did not consider the mortality differences obtained between age groups to be significant. Perhaps these differences would have been greater if the sexes had been considered separately in his experiments. Using the same technique as Morrison, McLeod (1944) found that susceptibility increased with age up to five days, which is the reverse of that found for DDT. Similarity in the results of the two investigations is hardly to be expected, however, since the insecticide, the application method, and the strain of flies were all different.

The significance of the correlation found between changes in respiration rate and in susceptibility to DDT with age is not clear because of the lack of information on the action and fate of DDT after absorption through the cuticle of *Drosophila*. In the case of the house-fly, however, there seems to be general agreement in the literature that absorbed DDT is partly metabolised into less toxic substances (see review by Babers & Pratt, 1951). Furthermore, Perry and Hoskins (1950) conclude that the ability of house-flies to metabolise DDT is a major factor in the individual variation in susceptibility. If similar processes occur in *Drosophila*, one possible explanation of the above correlation would be that an increased metabolic rate, as indicated by a rise in oxygen uptake, increases the ability of the flies to degrade DDT.

Summary.

DDT in odourless distillate was topically applied to individual males and females of the Rothamsted wild type of *Drosophila melanogaster* Mg. The lines for the regression of mortality in probits on log. dosage of DDT for males and females, five days old, were parallel, and males were 1·86 times as susceptible as females. Susceptibility was high in young flies, but rapidly decreased with age, to a minimum at about five days, thereafter increasing rapidly in males and not significantly in females. The need for sexing and standardising age in flies used for toxicological investigations was thus demonstrated.

Respiration rate in untreated flies was measured by a modified Barcroft method. In males it increased with age up to five days, and then decreased; in females it increased with age up to nine days. Variations with age in respiration rate and susceptibility to DDT were negatively correlated.

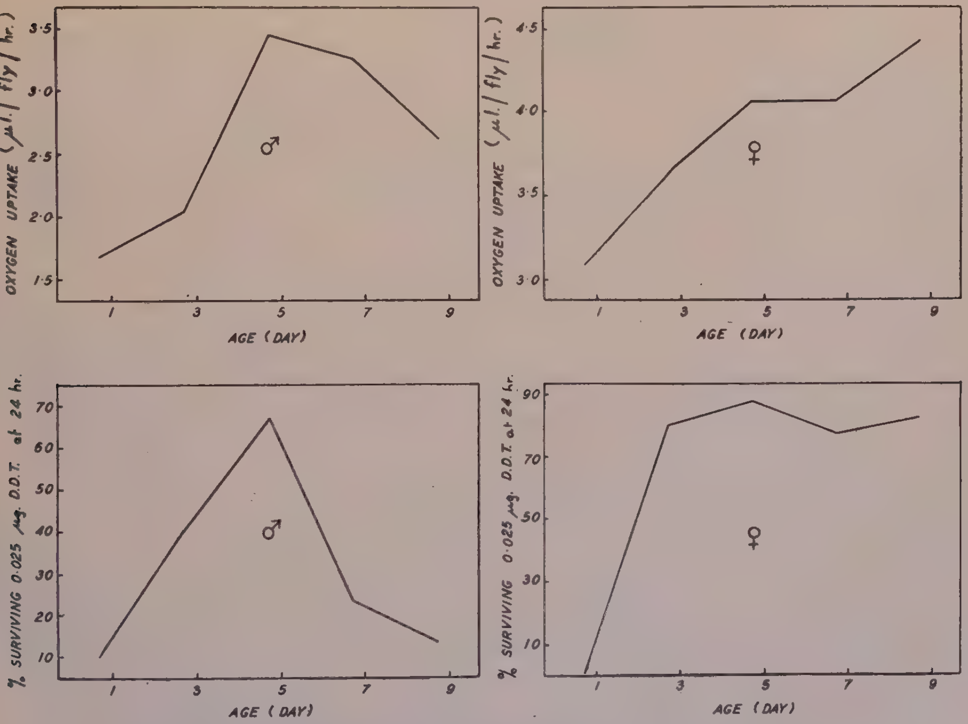


Fig. 1.—Comparison of effect of age on respiration rate of untreated flies and on survival of flies treated topically with a fixed dosage of DDT.

Acknowledgements.

I wish to thank Sir William G. Ogg, the Director of Rothamsted Experimental Station, for the opportunity of working at the Station for the period during which this investigation was carried out. I am grateful also to Dr. C. Potter, Head of the Insecticides and Fungicides Department, for making available the facilities of the Department, to Dr. F. Tattersfield for his suggestions regarding the programme of work, and his constant interest and encouragement during its progress, and to Dr. K. A. Lord for advice and assistance in the respiration study. Grateful acknowledgement is made of the help given by Miss J. Kerridge in the rearing of insects.

References.

Babers, F. H. & Pratt jr., J. J. (1951). Development of insect resistance to insecticides. II.—U.S. Dep. Agric. Bur. Ent., E-818, 45 pp., multigraph.

Dixon, M. (1934, 1951). Manometric methods.—London, Cambridge Univ. Press.

Finney, D. J. (1947). Probit analysis.—256 pp. London, Cambridge Univ. Press.

Kerr, R. W. (1951). Bull. sci. industr. Res. Org. Aust., no. 261, 63 pp.

Kerr, R. W. (1954*a*). Bull. ent. Res., **45**, pp. 313–316.

Kerr, R. W. (1954*b*). Bull. ent. Res., **45**, pp. 317–321.

L'Héritier, P. (1948). Heredity, **2**, pp. 325–348.

Lord, K. A. (1949). Ann. appl. Biol., **36**, pp. 113–138.

McLeod, W. S. (1944). Canad. J. Res., (D) **22**, pp. 87–104.

Morrison, F. O. (1943). Canad. J. Res., (D) **21**, pp. 35–75.

Perry, A. S. & Hoskins, W. M. (1950). Science, **111**, pp. 600–601.

Potter, C. (1941). Ann. appl. Biol., **28**, pp. 142–169.

Potter, C. (1952). Ann. appl. Biol., **39**, pp. 1–28.

THE FREEZING PROCESS OF FROST-HARDY CATERPILLARS.

By E. Asahina, K. Aoki and J. Shinozaki.
Institute of Low Temperature Science, Hokkaido University,
Sapporo, Japan.

(Plates XXXIII & XXXIV.)

It is well known that " cold hardiness " in insects is chiefly a matter of prevention of freezing. However, some insects especially those which pass the winter exposed to extremely low temperatures in a cold climate can withstand body freezing. Bachmetjew (1901) presented a theory of " Anabiosis " which means a maintenance of the structure of the organism without life processes. This theory was supported by Lozina-Lozinskiĭ (1937), whose conclusions were based on his observations on the survival of prepupae of the European cornborer after a " complete " freezing of protoplasmic water at temperatures below −20°C. So far as the writers are aware, the exact mechanism of such " frost resistance " has not yet been elucidated.

From investigations on the nature of cellular respiration in some caterpillars, Kozhantshikov (1938) suggested that at low temperatures the oxidase systems dependent on the integrity of the cell structure are replaced by the dehydrogenase systems which are not associated with structural elements of the cell, therefore the cell freezing may exert no harmful effects on the caterpillar. Although the insect body freezes hard, yet there is no reason to believe that in the insect the destruction of the cellular structures is always brought about by the crystallization of the water. Salt (1936) considered that in frost-hardy insects " death probably occurs either when a certain vital tissue becomes frozen, or when a certain degree of freezing is reached." To solve this complicated problem, it is necessary to observe directly the process of the freezing of the body, especially that of the cells of frost-hardy insects. The experiments reported in this paper were designed to clarify the freezing process in the tissue cells of the " frost-resistant " insects, in the hope that it would contribute to the understanding of frost-resistance mechanism.

Materials and Methods.

A common " slug caterpillar " in Japan, *Cnidocampa flavescens* (Walk.) * in various stages of its life cycle was employed as material. The adults of this Limacodid moth emerge in July and August, and the larvae from eggs laid by them become practically full-grown by September, when they construct hard oval cocoons. Soon after spinning cocoons they transform from larvae provided with a conspicuous armature of spine-bearing scoli to rather smooth-skinned prepupae. They overwinter as prepupae in their cocoons; pupation begins usually in June of the next summer. In the vicinity of Sapporo, the overwintering or hibernating period of this caterpillar may continue from November till April of the next spring, though the period of prepupal diapause may end at the beginning of December. The cocoons are found on the twigs or trunks of maple trees and remain usually uncovered by snow during the winter. Therefore they must be directly exposed to severe cold.

---

* The correct name is *Monema flavescens* Walk., the species having been first described in the genus *Monema* Walker, which is now recognised to be valid.—Ed.

Owing to their remarkable "frost-hardiness" and the softness of the body, the prepupal larvae in the cocoons are very convenient for experimental use. These larvae are entirely quiescent except for the peristaltic movement of the heart, visible through the dorsum, by which it can be easily determined whether they are alive or dead. More than two thousand cocoons were collected from the maple trees on which the caterpillars had been feeding, and were kept in a cage at outdoor temperature. Naked larvae from the cocoon usually ranged from 250 to 450 mg. in weight.

Body temperatures on each individual were taken galvanometrically with a thermocouple consisting of copper and constantan wire of 0·2 mm. diameter. The galvanometer deflection was directly read every 15 seconds or self-recorded. Special caution being taken not to pierce the body wall, the tip of the thermocouple was inserted in the pit of the larva (a fold which is formed in the anterior end of the prepupal larva by the partial retraction of the head into the body cavity) which was held in a small celluloid basket. The whole was then placed in a test tube (varying in diameter) which was immersed in a cooling bath at about −35°C. The freezing curves were drawn for each individual, and were used to estimate the undercooling point and the freezing time. Further, the effect on viability of the duration of the time for which the body was frozen was studied in the following manner. Ten intact cocoons were placed in a glass tube of which the diameter was just enough to allow the insertion of the cocoon, and those in eight glass tubes were subjected to freezing at −20°C., then stored at about −15°C. After the desired period of time—1, 3, 7, 14, 40, 75, 100, and 130 days respectively—the ten frozen insects in one of the eight glass tubes were then thawed at room temperature and mortality and further emergences from the prepupae were recorded. Besides these experiments the effect on the naked larvae of repeated daily freezing and thawing was studied.

At the same time direct observations of the freezing of dissected larvae as well as microscopical observations of the freezing processes of the blood and the tissue cells of the insect were made. In the latter case, a drop of blood or a small piece of tissue mounted in a small drop of liquid paraffin was subjected to freezing under a microscope in a special thermostat, while the temperature of the hanging drop was read with a small thermocouple during the course of the observation. In order to prevent excessive supercooling of the materials they were inoculated with a fine ice needle at the desired temperature.*

Freezing of the Intact Body.

The "slug caterpillar" is a typical "cold-hardy" insect belonging to the first group of Payne's classification (Payne, 1927). A clear periodicity in the undercooling points was found; they are high during the summer, drop during the autumn as the lower temperature arrives, reach a minimum during the winter, and rise again on the approach of higher temperature in the following spring, as shown in Table I.

A typical freezing curve of the naked prepupa of the overwintering stage is presented in fig. 1. (Details of the undercooling point and the freezing curve of the "slug caterpillar" at various seasons are to be found in Aoki & Shinozaki, 1953*a*.) In this stage the insects have usually recovered their heart beats after thawing of the body which had been frozen even at a temperature as low as about −30°C. In intact cocoons, the larvae can be frozen experimentally at a temperature below −20°C. in about forty minutes, and as a rule, on a cold winter morning when the atmospheric temperature approaches about −20°C., the larvae in the field certainly freeze. The insects could survive in a frozen state at about −15°C. for a period of more than 100 days, without any harm to their further development, and the newly hatched larvae from their eggs showed normal viability. Furthermore, daily freezing and thawing could be repeated many times without any lethal effect on the naked larvae. Even at a temperature of about 0°C., however, desiccation was so harmful to the larvae that in the open air the naked larvae could not withstand exposure for a few weeks.

---

* For details regarding the freezing apparatus consult Asahina (1950).

Most of the larvae during the warm seasons, on the contrary, cannot survive after a freezing period of a few days at −10°C. But if the freezing temperatures

TABLE I.

Seasonal variation of the undercooling point.

Stage	Season	Undercooling point (° C.)	Number of insects used
Full-grown larvae ..	September	− 4·9 ± 1·2	11
A few weeks after spinning cocoon ..	September	−12·2 ± 2·3	12
Prepupae	October	−15·4 ± 1·3	8
,, ...	December	−21·5 ± 3·5	11
,, ...	February	−25·2 ± 2·3	12
,, ...	March–April	−19·2 ± 2·4	45
,, ... (near pupation)	May	−13·5 ± 2·4	10

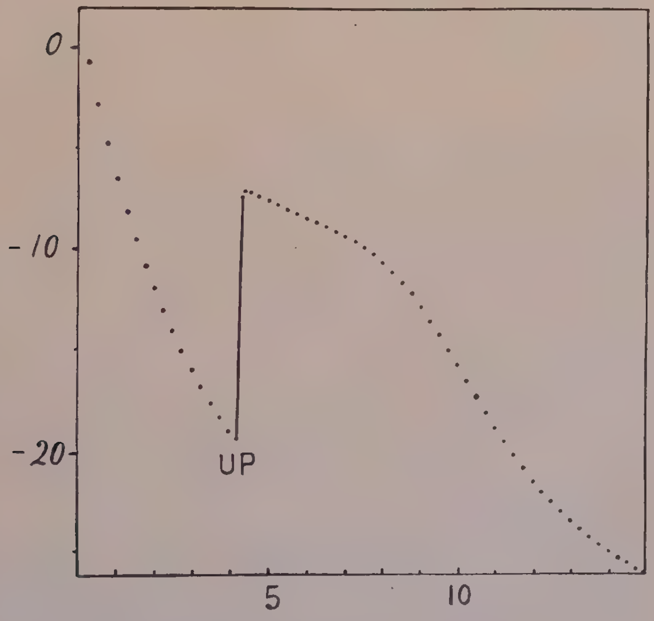


Fig. 1.—Freezing curve of an overwintering prepupa, 18.iv.1951. Ordinate, temperature in °C.; Abscissa, time in minutes; UP, undercooling point.

are not too low and the duration of the freezing period is very short, the congelation of these larvae usually does not cause death. In Table II some of these data are presented in a condensed form.

TABLE II.

Frost-resistance of the larvae at various seasons.

Stage	Date	Undercooling point (°C.)	Final body temperature (°C.)	Duration of freezing (min.)	Results
Feeding larva	5. ix	− 4·2	− 4·0	8	alive
,, ,, ...	8. ix	− 4·7	− 5·8	11	dead
Two weeks after spinning	10. ix	−10·2	− 4·8	6	alive
,, ,, ,, ,,	10. ix	−15·3	−17·7	11	dead
Prepupa	24. x	−15·9	−15·0	16	alive
,, ...	19. xii	−24·0	−31·7	10	alive
,, ...	28. iv	−20·7	−28·7	16	alive
,, ...	2. v	−17·0	− 9·3	5	alive
,, ...	20. v	—	−10·0*	300	alive
A few days before pupation	12. vi	—	− 5·0*	15	dead

* Air temperature near the insect.

Freezing of the Blood.

In the prepupal stage of the "slug caterpillar" most of the body cavity is filled with the fat body and blood. About 45 per cent. of the total body weight of such a hibernating larva is occupied by the blood, of which about three-fourths is pure water (Table III). It is natural to expect that the freezing of the blood should play an important part in the freezing process of the insect, because the blood is supposed to be set free from a supercooled state more easily than the tissues.

The blood obtained from a dissected larva by a fine glass pipette was put into a small test tube and cooled slowly in a cooling bath at about −5°C. Preventing excessive supercooling by the inoculation with ice, the freezing point of the blood was individually measured with a thermocouple. To maintain the blood at uniform temperature, it was continuously agitated during the determination. From the results obtained there was found to exist a correlation between the freezing points of the blood and the undercooling points of the intact larvae (Tables I and III). Certainly the blood has a considerable capacity for supercooling. It is, however, very doubtful whether or not this property of the blood is the sole factor that determines the supercooling phenomenon of the insect (Aoki & Shinozaki, 1953*b*).

In actively feeding larvae, the freezing point of the blood is apparently high, it becomes somewhat lower, however, as soon as the larvae begin to spin their cocoons, and drops during the autumn. The maximum depression in the freezing point of the blood is observed in overwintering prepupae; this freezing point rises again in the following spring.

Despite the fact mentioned above, no intimate relation between the freezing point and the water content of the blood is found. For instance, just at the time of spinning of the cocoon the blood temporarily becomes very sticky and its water content is distinctly lower than that of the larvae of two weeks later when the freezing point of the blood shows a somewhat lower value than that at the spinning time.

On the other hand, there is no fundamental difference between the form of ice crystal of pure water and that in the caterpillar blood. The rate of crystal growth in the blood, however, is very much slower than in pure water owing probably to the existence of a large quantity of colloidal materials in the blood.

TABLE III.

Relation between the freezing point of the blood and the water content.

Stage	Season	Freezing point of the blood (°C.)	Number of insects used	Water content %	
				Blood	Whole body
Feeding larva ..	September	−0·75 ± 0·06	9	89·6	80·5
Spinning of cocoon	September	−0·93 ± 0·07	5	70·3	66·4
Two weeks after spinning ..	September	−1·11 ± 0·06	10	77·5	65·2
Prepupa	February–March	−2·04 ± 0·15	22	74·2*	60·9*
Prepupa	May	−0·72 ± 0·03	10	—	—

* In this case, the measurement of water content was made only at the beginning of March using 18 prepupae.

After thawing no changes in the blood caused by the freezing, if for a short period of time, are observable. Upon inoculation, the ice originates from discoid shaped germs (foci) and grows to hexagonal fern-like crystals (Pl. XXXIII, fig. 3). In the blood of larvae in the summer stage, the dendritic ice crystals rapidly fuse with each other resulting in an embedding of condensed blood in the ice mass, consequently many vein-like branches or droplets of the blood are trapped (Pl. XXXIII, fig. 1). In the blood of hibernating prepupae, the ice grows very slowly and the condensed blood is not usually embedded in the ice, since the branches of the ice crystals do not fuse into a large ice mass (Pl. XXXIII, fig. 2). In such a case, around the contours of the ice crystals a dark area which is attributable to the condensation of blood is usually recognised after a rapid thawing of the ice. The formation of such a layer of condensed blood is quite reversible in the repetition of freezing and thawing. It is thus obvious that if the formation of such a condensed blood layer plays some role in the frost resistance of the insects, this advantageous function of the blood is most effectively performed in the body at the overwintering stage.

Freezing Process of the Dissected Body and the Isolated Tissues.

The overwintering prepupae having been dissected along the median line of the ventral side, they were laid on their backs and directly exposed to a temperature of −10°C. in a cold chamber. The first visible change is the initiating of freezing of the blood at a few points on the blood surface, which is probably due to inoculation with frost crystals floating in the air of the cold chamber. When once a crystal is formed in the blood it grows radially until the whole space, which has been filled with blood, is occupied by feather-like ice crystals. Around these the blood is condensed as a yellow gelatinous mass. The condensed blood has the appearance and rigidity of a weak gelatin gel. Although an exposure to −10°C. solidifies the frozen body quite hard, the dissected prepupae withstand severe freezing even at −20°C. for at least one hour without any gross abnormalities in the body organs, and the heart beat always recovers after thawing.

For the observation of the freezing processes of organs, the isolated heart or the dorsal vessel was chiefly used, because its active contraction easily demonstrates the recovery of viability. The heart, removed and immersed in the blood, maintained its peristaltic movement, though sometimes irregular, at room temperature for more than three days, and in sodium chloride solutions of 0·59 gram molecules per litre (M) and 0·15 M, for at least three hours and one hour, respectively. Further, the freezing process of the pericardial and the fat body cells was carefully observed. These isolated organs, such as heart, fat body, ventral nerve cord and gonad, surrounded with blood, being under conditions of supercooling, were inoculated with ice at desired temperatures. The freezing starts from the inoculated point, and the ice grows gradually around the organ till the whole tissue is tightly wrapped with ice. Even if the freezing occurred at a low temperature of more than −20°C., no gross changes took place in the frozen tissue of the hibernating insect (Pl. XXXIV, fig. 1), except that the size of the organ often seemed to become somewhat smaller than before. In organs frozen in this way a shrinking of the tissue cells was usually observed because of the dehydration caused by the ice growing on the cell surface. Such a remarkable shrinking of the pericardial cells is represented in Plate XXXIII, fig. 5. On the surface of fat body, the ice usually grows along the border line of each of the cells which constitute the cell layer of the organ (Pl. XXXIV, fig. 6). After thawing, most of the cells appeared to be quite normal. When these cells have been vitally stained* before freezing, no changes of coloration of the cells were observed. The isolated heart always recovered the contractile movement even after a severe freezing at −20°C. for at least 15 minutes.

Judging from our experimental work on the freezing processes of many kinds of plant- or animal-cells, the cells frozen intra-cellularly are usually darker than those unfrozen, and cells frozen in this way never shrink (Asahina, 1948, 1953*a*; Aoki, Asahina & Terumoto, 1953). From the results mentioned above one infers that in hibernating prepupae most of the tissue cells are usually frozen extra-cellularly. On the other hand the cells of these insects, when washed with hypotonic salt solution before freezing, can be easily frozen intra-cellularly. After immersion in 0·15 M sodium chloride solution for 30 minutes, the isolated heart was subjected to freezing in the same way. At a temperature below −15°C., the whole organ became quite dark (Pl. XXXIV, fig. 2) as soon as the organ was wrapped in ice, and the pericardial cells attaching to the heart surface froze simultaneously in flashes, with a resultant intense darkening as shown in Plate XXXIII, fig. 6. Immediately after the flashing mentioned above, a large number of minute ice crystals embedded in coagulated cytoplasm were observed in cells frozen in this way, but these soon fused into larger ice masses (Pl. XXXIII, fig. 4). A heart thus frozen has entirely lost its viability and the cell protoplasm has usually coagulated, though no apparent change was observed in the cell form after thawing.

The same freezing process takes place in the cells of insects during summer. At the stage near pupation, the organs removed from the prepupae froze intra-cellularly unless the freezing was done at a temperature not lower than −5°C. After thawing, a remarkable destruction of the cell structure usually took place. Immediately after freezing at −10°C., the free-floating fat cells in the blood of pupae (Pl. XXXIV, figs. 3, 4) always collapsed entirely as shown in Plate XXXIV, fig. 5.

Additional Observations on Caterpillars of several other Species.

The expectation that the freezing process mentioned above might occur in other insects having similar structure, led the writers to experiment on caterpillars of some other species, the results of which are presented in Table IV. These larvae, having been under conditions of supercooling, were frozen artificially by touching with an ice crystal and then exposed in the thermostat to desired temperatures. The listed temperatures, therefore, do not always represent the body temperatures. As is clearly noted in Table IV, these larvae in the stages near the overwintering period are very resistant to body freezing.

---

* Neutral red with methylene blue was used.

TABLE IV.

Frost-resistance of some other caterpillars.

Species	Stage	Date	Temperature exposed (°C.)	Duration of freezing	Results	Number of insects used
Pyrausta nubilalis (Hb.)	Overwintered larvae	7. iv	−20	4 hrs.	alive	10
Pyrausta nubilalis (Hb.)	Overwintered larvae	9. iv	−15	2 days	alive	10
Pyrausta nubilalis (Hb.)	Full-grown larvae	2. ix	−10	10 min.	dead	5
Agrotis segetum (Schiff.) ..	Overwintered larvae	9. iv	−10	15 hrs.	alive	6
Agrotis segetum (Schiff.) ..	Overwintered larvae	16. v	− 2	40 min.	alive	4
Agrotis segetum (Schiff.) ..	Larvae of 3–5 stage	17. vii	−10	1 hr.	dead	7
Agrotis segetum (Schiff.) ..	Full-grown larvae	21. viii	− 5	10 min.	alive	5
Mythimna grandis Butler ..	Overwintered larvae	16. iv	− 3	50 min.	alive	3
Xylena fumosa (Butler) ..	Full-grown larvae	7. vii	− 3	5 min.	alive	5

In material which has overwintered in soil in the field, the larvae of the Turnip Moth, *Agrotis segetum* (Schiff.), collected after the melting of snow cover, can withstand all night the solidification of the body. Even in late spring, if the degree of freezing is very low, the actively feeding larvae of *Mythimna grandis* Butler, a moth allied to the Double Line, *M. turca* (L.), which occurs in Britain, can also be frozen without any harmful effects on their viability. Also in midsummer, the full-grown larvae of the Sword-grass, *Xylena fumosa* (Butler), as well as of *Agrotis segetum* of the same stage, could survive after a body freezing of very short duration. Moreover, it may be of interest that the imago of the Copper Underwing, *Amphipyra pyramidea* (L.), recovered its flying activity after it had congealed quite hard for five minutes, although one night later this moth died.

In the caterpillars mentioned above, after thawing, the organs of the larvae that survived retained their normal appearance. However, when the active summer larvae were subjected to freezing at a temperature lower than −10°C., their tissues usually froze intra-cellularly. For instance, the organs removed from full-grown larvae of *Agrotis* became highly opaque as soon as the freezing took place, and some of them were broken down soon after thawing.

Discussion and Conclusion.

Modes of cell freezing in the frost-hardy insect.

As has been well known, when plants withstand freezing the ice crystallisation always takes place only at the outside of the protoplast, *i.e.*, extra-cellular freezing occurs (see Levitt, 1941 pp. 15–18). As far as our earlier experiments are concerned, the cells frozen intra-cellularly never survive after thawing (Asahina, 1948; Aoki, Asahina & Terumoto, 1953).

In a previous paper it was suggested that in the tissue of frost-hardy insects extra-cellular freezing occurs easily (Asahina & Aoki, 1951). The present observations seem to support the correctness of that suggestion. At least at temperatures higher than −20°C., the tissues removed from the overwintering " slug caterpillar " always froze extra-cellularly, and when thawed, cells frozen in this way usually recovered their normal appearance. When it has been frozen, the heart could regain the characteristic movement after thawing. No abnormalities of any kind were found in the tissue cells of thawed larvae which, in any case, had withstood body freezing.* On the other hand, the heart in which intra-cellular freezing had occurred never recovered its activity and in cells so frozen a coagulation of protoplasm always took place. Some of the tissue cells of the summer insects, which cannot withstand body freezing at −10°C. usually underwent intra-cellular freezing at that temperature.

Such experimental evidence shows clearly that in general the cells of frost-resistant insects freeze extra-cellularly, and in insects frozen in this way destruction of the cellular structures which has been suggested by Kozhantshikov (1938) is not expected. Moreover, from the present observations it seems quite probable that the extra-cellular freezing in the tissue is a rather general phenomenon in insects, at least of certain types, if the freezing temperature is not too low. In such a case the ice formation in the insect, if for a short time, even when its body becomes quite hard, is not always fatal to the insect in the summer stage, in which most insects have been regarded by some investigators to be killed as soon as their tissues freeze (see Wigglesworth, 1950, p. 444). But for a longer period of freezing this is not the case. In the " slug caterpillar " the prepupae are not usually killed at the end of May by freezing for a few hours only, whereas body freezing for a few days is quite harmful to them. This phenomenon, however, is not always due to Payne's " quantity factor of cold " (Payne, 1928), since the insect can always withstand the far longer exposure to cold, if it is merely under conditions of supercooling. As has been noted in plant cells (Siminovitch & Levitt, 1941), insects of less hardiness must be seriously affected by the length of time of the extra-cellular freezing of the tissue cells.

Probable freezing process of the overwintering caterpillars in natural conditions.

As has been stated by many authors (see Wigglesworth, 1950, p. 445), the state of supercooling of overwintering insects is very stable. There are, however, in nature many causes to induce freezing in insects which are in a sufficiently supercooled condition, such as an exposure to extremes of winter temperatures, an intimate contact of body surface with ice crystal and, sometimes, mechanical shocks. The very compact cocoon of the " slug caterpillar " provides a particularly favourable covering for the prevention of inoculation with ice (Aoki and Shinozaki, 1953*b*). In any case when the insect body is freed from a supercooled state, it seems very probable that almost all of the ice may be produced in the blood at least in the beginning of the process, since the blood is regarded to be more freezable than any other tissues. Our observations suggest that in insect tissue the prevention of the freezing of the cell interior is very much favoured by the freezing of a large quantity of blood prior to the cell freezing. In other words the freezing of the blood lessens the degree of supercooling of the cells and decreases temporarily the cooling rate. This is also expected from the freezing curve of the prepupa (fig. 1).

---

* An exception was observed in fat body. When frozen near −40°C. for one hour the prepupae regained, perhaps temporarily, their heart beat after thawing. However, in the cells of the fat body the small fat granules of uniform size usually fused into larger homogeneous masses.

Besides, the blood seems to have some characters favourable to the prevention of the intra-cellular freezing of the tissue cells which are bathed in it. Kistler is quoted by Salt (1936) as having pointed out that ice crystals forming in solutions rich in hydrophilic colloids were liable to become covered with a sheath of dehydrated colloid, and thus they failed to " seed " the entire solution. These hypotheses were introduced by Salt (1936) in an explanation of the freezing process of insects, though he has not yet published any actual studies on this problem so far as the present writers are aware. As was stated in detail in the previous paper (Asahina, 1953*b*), the formation around the ice crystals of a condensed blood layer in which a large quantity of hydrophilic colloids is contained, was obviously demonstrated in the freezing process of the insect blood. Such a layer may not only retard the propagation of freezing, but effectively conceal the surface of the growing ice fronts in the body cavity, so that ice crystals can hardly be in direct contact with the cell surface. According to the senior writer's observations on the freezing process of plant- and animal-cells (Asahina, 1948, 1950, 1953*b*), without contact of the cell surface with ice the initiation of the freezing of the living cell interior is always much more difficult, even when the cell is mechanically jarred, than when the cell surface is in intimate contact with ice.

In addition there is another important factor that prevents the freezing of the cell interior. Even in the organisms of very low frost-hardiness, such as fresh water amoebae or algae of active stage, the protoplasmic surface layer of their cells has usually some ability to prevent the transmission of freezing into the supercooled cell interior (Chambers & Hale, 1932). In frost-hardy insects, it is to be expected that this advantageous function of the cell surface is much more highly developed. Indeed, after the washing in 0·59 M sodium chloride solution* to avoid the protective function of the blood, the isolated heart of the overwintering " slug caterpillar " froze extra-cellularly, and after thawing it recovered the contractile movement, even when the freezing had occurred at a low temperature of about −23°C. If the freezing temperature was higher than −10°C., the hearts treated even with a very hypotonic 0·15 M sodium chloride solution also froze in the same manner and most of them recovered their activity.

It therefore seems reasonable to assume that in overwintering caterpillars the tissue cells hardly freeze intra-cellularly, at least at the beginning of the process. When once extra-cellular freezing takes place, the tissue cells should undergo a dehydration and contract as the freezing proceeds further, unless the cooling is extraordinarily rapid. In cells frozen in this way, as already demonstrated in frost-hardy plant cells (Scarth, 1941), the water-holding capacity in cytoplasm must be very strong, although most of such water is not regarded as so-called bound water.

In view of the frost-resistance mechanism described above, it may be suggested that in the body of frost-hardy insects only blood and the water drawn from the cell interior freeze and in general the cell itself or the cell interior is free from freezing, and that the "anabiotic" state (Bachmetjew, 1901) of a frozen insect is certainly accompanied by neither the destruction of cell structure nor the complete freezing of protoplasmic water.

---

* The freezing point depression of this solution is approximately equivalent to that of the blood of overwintering " slug caterpillar."

Summary.

Using mainly the overwintering prepupae of a "slug caterpillar", *Cnidocampa flavescens* (Walk.), the mechanism for the frost-resistance in insects was investigated.

Though the freezing point of the blood shows the value of about −2°C. the prepupae are very readily supercooled. When cooled below −20°C., however, the insect body suddenly congeals hard. Insects frozen thus, even for a long period of 100 days, usually withstand the solidification of their bodies without any harmful effect upon either the further development or upon the next generation.

Judging from the shape of the freezing curves of the prepupae and the freezing processes of the blood and isolated tissues, it is inferred that the most probable freezing process of the caterpillar is as follows. At first, the blood freezes rapidly, and consequently the grade of supercooling of the tissue cells is very much lessened by the latent heat of fusion of ice. Extra-cellular freezing of the tissue cells then takes place, in which case the properties of the blood as well as some property of the plasmic surface layer of the cells may play an important role in the prevention of the transmission of freezing into the cell. With the advance of the blood freezing, the tissue cells undergo dehydration and contraction; nevertheless, they usually withstand such a condition for a long period, provided that the freezing temperature is not too low. Consequently, the so-called anabiotic state of a frozen insect does not necessarily mean the destruction of the cell structure.

According to the writers' studies on several other insects of various degrees of cold-hardiness, the freezing process described above seems to be a rather general phenomenon at least in certain types of insects, although non-hardy insects are very susceptible to the time factor of body freezing as well as to the "intensity factor of cold."

Acknowledgement.

The authors wish to acknowledge their indebtedness to Prof. V. B. Wigglesworth who has kindly read through the manuscript.

References.

Aoki, K., Asahina, E. & Terumoto, I. (1953). The relation between the shape of the freezing curve and the frost-hardiness of red beet.*—Low Temp. Sci., **10,** pp. 87–100.

Aoki, K. & Shinozaki, J. (1953*a*). On the undercooling of the prepupa of slug moth.*—Low Temp. Sci., **10,** pp. 127–134.

Aoki, K. & Shinozaki, J. (1953*b*). Effect of cooling rate on the undercooling points of the prepupa of slug moth.*—Low Temp. Sci., **10,** pp. 135–143.

Asahina, E. (1948). Freezing process of the "sap drop type" of flashing in plant cells, with reference to the plasmolysis resulted from ice formation in the cell.*—Low Temp. Sci., **4,** pp. 85–96.

Asahina, E. (1950). Microscopical observation of the freezing process in the parenchyma of plants.*—Low Temp. Sci., **8,** pp. 229–246.

---

* In Japanese with English summary.

Asahina, E. (1953*a*). Freezing process of egg cell of sea urchin.*—Low Temp. Sci., **10,** pp. 101–113.

Asahina, E. (1953*b*). Freezing process of blood of a frost hardy caterpillar, *Cnidocampa flavescens*.*—Low Temp. Sci., **10,** pp. 144–153.

Asahina, E. & Aoki, K. (1951). Some notes on the freezing process of frost-hardy insects.*—Kontyu, **19,** pp. 13–18.

Bachmetjew [Bakhmet'ev], P. (1901). Experimentelle entomologische Studien vom physikalisch-chemischen Standpunkt aus., **1,** 160 pp. Leipzig.

Chambers, R. & Hale, H. P. (1932). The formation of ice in protoplasm. Proc. roy. Soc., (B) **110,** pp. 336–352.

Kozhantshikov, I. W. [Kozhanchikov, I. V.] (1938). Physiological conditions of cold-hardiness in insects.—Bull. ent. Res., **29,** pp. 253–262.

Levitt, J. (1941). Frost killing and hardiness of plant. Minneapolis.

Lozina-Lozinskiĭ, L. K. (1937). Cold-hardiness and anabiosis in larvae of *Pyrausta nubilalis*.—Zool. Zh., **16,** pp. 614–642. [In Russian with English summary.]

Payne, N. M. (1927). Freezing and survival of insects at low temperatures. —J. Morph., **43,** pp. 521–546.

Payne, N. M. (1928). Cold hardiness in the Japanese beetle, *Popillia japonica* Newman.—Biol. Bull., **55,** pp. 163–179.

Salt, R. W. (1936). Studies on the freezing process in insects.—Tech. Bull. Minn. agric. Exp. Sta., no. 116, 41 pp.

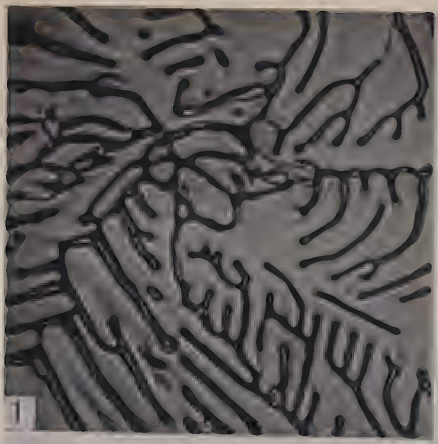
Scarth, G. W. (1941). Dehydration injury and resistance.—Plant Physiol., **16,** pp. 171–179.

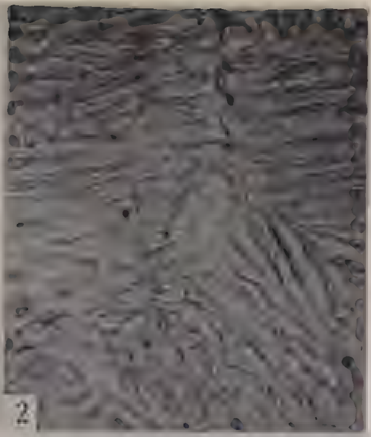
Siminovitch, D. & Levitt, J. (1941). The relation between frost resistance and the physical state of protoplasm. II. The protoplasmic surface.—Canad. J. Res., (C) **19,** pp. 9–20.

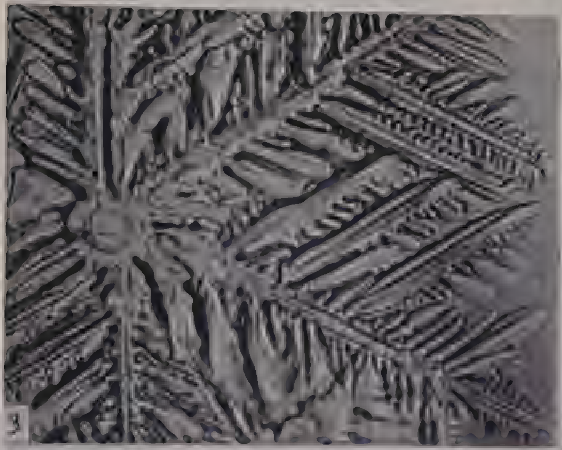
Wigglesworth, V. B. (1950). The principles of insect physiology.—4th edn., 544 pp. London, Methuen.

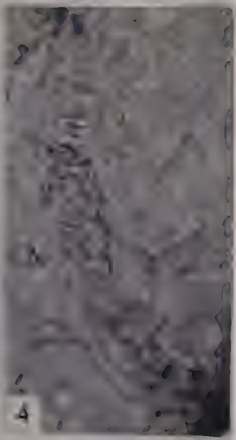
---

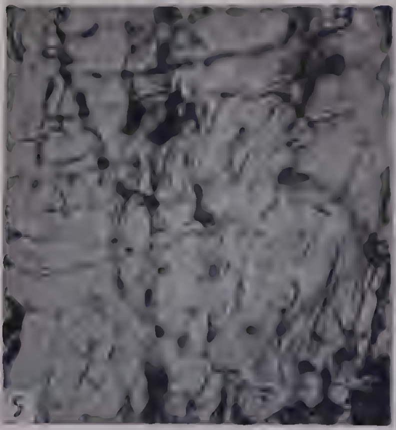
*In Japanese with English summary.











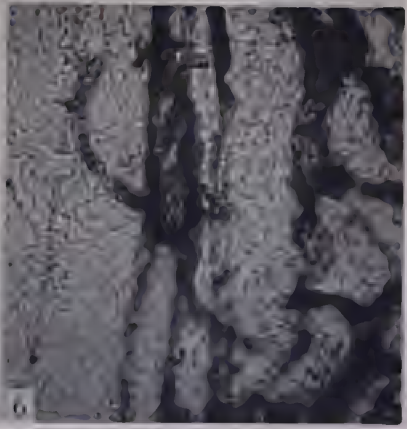


FIG. 1. Frozen blood of the summer larva, 3 days after the spinning of cocoon; photograph taken at –8° C. (x 88).

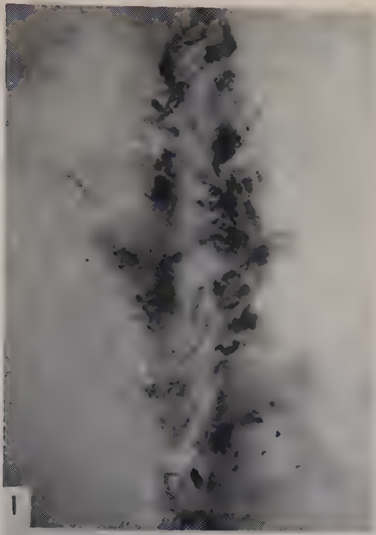
FIG. 2. Blood of the overwintering prepupa frozen at –20° C.; photograph taken at the same temperature. (x 306).

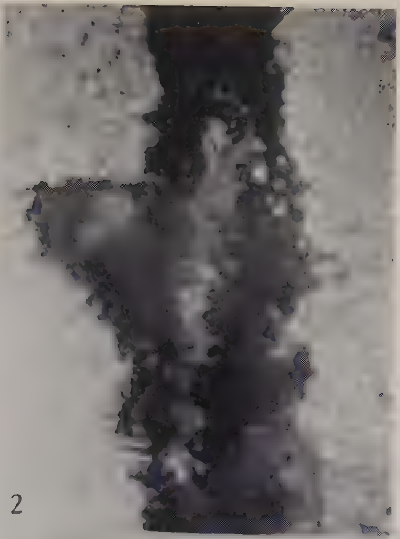
FIG. 3. Ice crystal formed in the blood of overwintering prepupa; photograph taken at –2·8° C., one minute after the inoculation with ice at –2·6° C. (x 88).

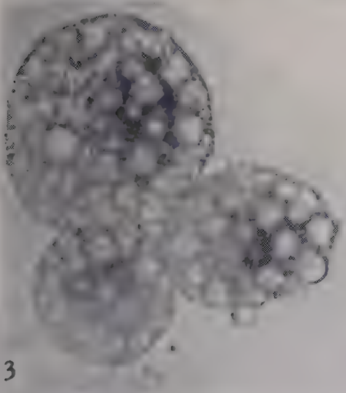
FIG. 4. Details of fig. 6 (below) showing the cell interior, eleven minutes after the intracellular freezing at –10° C. (x 306).

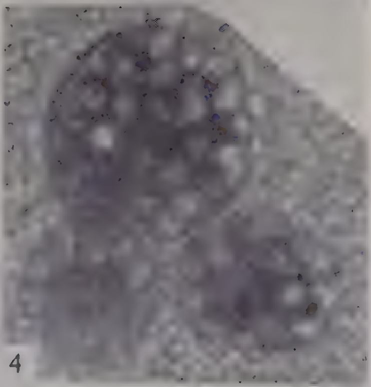
FIG. 5. Pericardial cells with alary muscle frozen extra-cellularly at –4·2° C. (x 88).

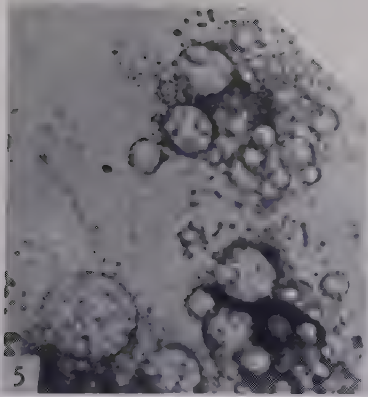
FIG. 6. Pericardial cells with alary muscle frozen intra-cellularly showing the remarkable darkening of cell interior at –10° C. (x 88).











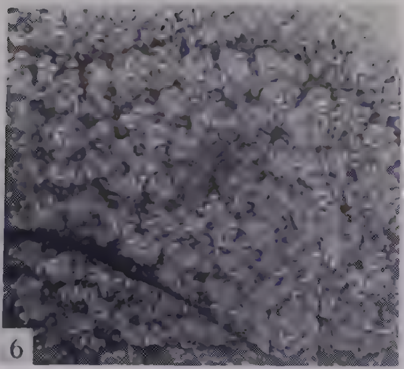


FIG. 1. Isolated heart with vitally stained pericardial cells of overwintering prepupa frozen with blood. The tissue somewhat contracts owing to the dehydration by ice formation. (x 28).

FIG. 2. Isolated heart with vitally stained pericardial cells of overwintering prepupa washed previously in 0·15 M NaCl solution and frozen at –20° C. The tissue appears very dark but never contracts. (x 28).

FIG. 3. Free-floating fat cells in the blood of pupa. (x 306).

FIG. 4. Free-floating fat cells in the blood of pupa after intra-cellular freezing at –9° C. (x 306).

FIG. 5. Destroyed fat cells, just thawed after the freezing at –9° C. for ten minutes. (x 306).

FIG. 6. Fat body of overwintering prepupa frozen extra-cellularly showing the ice formation of the border line of the cells at –13° C. (x 118).

OBSERVATIONS ON THE LIFE HISTORY OF *LAEMOPHLOEUS MINUTUS* (OL.) (COL. CUCUJIDAE) WHEN BRED ON VARIOUS STORED CEREALS AND CEREAL PRODUCTS.

By Gwyneth C. Williams.
Ministry of Agriculture and Fisheries,
Infestation Control Division.

Species of *Laemophloeus* occur commonly on a large variety of stored products and have been reported from widely separated parts of the world. The distribution of three closely related species, *L. minutus* (Ol.), *L. ferrugineus* (Steph.) and *L. turcicus* Grouv., has already been reviewed by Davies (1949), who also discusses the biology of *L. minutus*.

Insects in this genus are well-known pests of grain and are of particular importance when associated with the heating of bulk wheat (Howe, 1943; Oxley & Howe, 1944). Their status as major pests of grain in the United Kingdom has been described by Freeman (1952). In the present work an attempt is made to determine the factors influencing the development of one species, *L. minutus*, on a number of commercial grains and grain products, namely, English and Manitoba wheat, Plate maize, and wheat flours of three different extraction rates, wholemeal, National (85 per cent. extraction) and Canadian (70–75 per cent. extraction), respectively.

In view of the discovery by Lucas and Oxley (1946) of a species closely resembling *L. minutus*, since described by Steel and Howe (1952) as *L. pusilloides*, the genitalia of a large number of specimens drawn from the stock cultures were examined to confirm that the species used in the present studies was, in fact, *minutus*. Without exception it was found that the structure of both male and female genitalia tallied exactly with those figured by Reid (1942) for *L. minutus*.

Life History and its Relation to Diet.

The life history of *L. minutus* as observed by Davies (1949) comprises four larval instars. The late fourth-stage larva enters a distinct prepupal phase during which a cocoon is formed of silk extruded from a pair of mamilliform silk glands situated in the prothorax. The prepupa moults within the cocoon to give rise to the pupa.

In order to decide which of a variety of foodstuffs provides the most suitable diet for the development of the species and to estimate the rate of increase in infestation liable to occur on any one of them, it would be necessary to compare the duration of the life cycle and mortality, together with the rate of egg-laying, associated with each medium. In the present studies, only the first two factors are considered.

Comparison of the rate of development was made by observation of mass cultures set up on each food material and incubated in constant conditions of 28°C. and 75 per cent. R.H. All food was sterilised and "conditioned" to the environmental conditions used throughout before being placed in $2 \times \frac{3}{4}$ in. tubes at the rate of 1 gm. per tube. Twenty eggs, drawn from a batch laid within the 24 hours immediately before setting up the experiment by a large number of adults taken from the stock cultures, were introduced to each tube.

The tubes, grouped in fives, were divided into two series. Series I was incubated until pupation occurred and then examined daily for the removal of newly emerged adults. In Series II a different group was examined every seven days until the life cycle was complete. The mean duration of the life-history on each medium was thus obtained, supplemented, from Series II, by information on the relative numbers of the various instars present at weekly intervals and differences in the course of development.

Statistical Analysis.

The experiments were so designed as to permit treatment of the data by an analysis of variance, followed by a comparison of means by the method of Tukey (1943). An inverse sine transformation was applied to data in the form of percentages in order to equalise variances. The well-known Chi-squared test was also employed where appropriate.

Duration of Life Cycle.

The results from Series I showed that the mean duration of the life-history agreed closely on Manitoba wheat and National flour and was shorter on these foods than on any of the other four. The longest period for egg to adult development was on Canadian flour, in which case the mean duration of 43·4 days was 9·2 days longer than on the shortest, Manitoba wheat. Statistical treatment of the figures by an analysis of variance, using the combined results for both sexes, shows that the period of development only on Canadian flour differed significantly from that on the other five media. A further analysis of variance, using the individual figures for males and females, showed no significant difference between the sexes in the completion of egg to adult development (Table I).

TABLE I.

Duration of the life history of *L. minutus* in association with various food media.

Food	Duration in days (range)	Mean duration (days)			Source of variation	F.	P.
		♂	♀	combined			
Manitoba wheat ..	29–50	34·83	33·20	34·27	Food ..	6·81	<0·001
English wheat ..	32–52	37·23	37·07	37·13	Sex ..	0·66	>0·02
Plate maize ..	31–60	39·00	38·90	38·83			
Wholemeal flour ..	31–51	37·00	35·23	36·07			
National flour ..	31–47	35·20	34·20	34·30			
Canadian flour ..	35–57	43·10	43·50	43·40			
		Least significant interval (P=0·015)		4·84			

Horizontal lines in column 5 separate groups differing significantly from each other but not within themselves.

The detailed observations in Series II indicated that prolongation of the life cycle on Canadian flour occurred in the fourth and later instars rather than earlier. Prepupae and pupae were not found until the end of 35 days on this food, whereas they had appeared by the 28th day on all the others. Unfortunately, the small number of adults emerging on Canadian flour made comparison with the more favourable foods difficult but no adult emergence was recorded until the 42nd day on this food whereas it was complete, or nearly so, on the remainder after the same period.

Mortality.

It might be assumed from the above results that Manitoba and English wheats, Plate maize and wholemeal and National flours form equally good media for the development of *L. minutus*. Reference to Table II indicates, however, that there is considerable variation in the total mortality on the six foods and that a short life history may be associated with high mortality, as in the case of National flour, thus influencing the order in which the foods may be placed as suitable for the development of the species.

TABLE II.

Mortality of *L. minutus* associated with various food media.

Food	Mean mortality %	Degrees Inverse sine transformation	P.
Wholemeal flour ..	16·7	23·93	<0·001
Manitoba wheat ..	20·7	27·03	
Plate maize	30·7	33·57	
English wheat	60·0	50·77	
National flour	78·7	62·53	
Canadian flour	84·7	66·93	
	Least significant interval (P=0·05)	7·12	

Horizontal lines in column 3 separate groups differing significantly from each other but not within themselves.

When the mortality figures are submitted to an analysis of variance, it is seen that they fall into four groups which differ significantly from each other, but not within themselves, namely, wholemeal flour and Manitoba wheat with the lowest mortality, followed by Plate maize, then by English wheat and, finally, National and Canadian flours with the highest death rate. As there is also no difference in the duration of the life cycle on wholemeal flour and Manitoba wheat, it can be said that these two media provide equally suitable diets and are more favourable for the development of the species than the remaining foods under consideration. Similarly, there is no significant difference in the length of the developmental period on English wheat and Plate maize but, when overall mortality is considered as well, it indicates clearly that the maize is a more favourable food than English wheat.

It should be borne in mind that crushed maize was used and it is possible that identical results would not be obtained with whole grains. In fact, Rilett (1949) found that populations of *L. ferrugineus* increased more rapidly on coarsely ground American corn than on whole grains and it may well be that *L. minutus* would show similar variation. Rilett also found that the development of *L. ferrugineus* on certain types of whole wheat was quicker than on crushed samples of the same varieties but, as already mentioned, the present work indicates that at least whole Manitoba wheat and ground wheat in the form of wholemeal flour are of equal value to *L. minutus*.

Canadian flour was clearly the least suitable of the six media as it produced both the longest life cycle and the highest mortality. National flour proved as poor as Canadian as regards mortality, but not period of development. It seems, therefore, to fall between English wheat and Canadian flour in order of preference.

The observations in Series II show striking variation in the stage at which mortality, when it occurred to a marked degree, was evident on the different foods. For instance, it was most apparent amongst first instar larvae on English wheat, but amongst fourth and later instars on National and Canadian flours. The latter was doubtless the result of nutritional deficiencies but, as will be shown later, the former appeared to be caused by mechanical difficulty in reaching a food supply. It was observed on both types of wheat that the larvae fed almost exclusively on the germ and that, once established in this region, mortality was low. Access to the germ of Manitoba wheat was, on the whole, easy for young larvae owing to the extensive damage to the overlying pericarp and testa of a high percentage of grains. In the English wheat, however, a much higher proportion of grains were undamaged in the vicinity of the germ and high mortality amongst newly hatched larvae apparently resulted from their being unable to penetrate the undamaged testa and reach the food they required.

Similar results were recorded by Davies (1949) who found that *L. minutus* adults cannot live on undamaged wheat grains but can only make their way into those with blemishes in the covering. In addition, Fraenkel and Blewett (1943) showed that larvae of other stored products pests are unable to survive on completely undamaged wheat grains and Rilett (1949) reported that young larvae of *L. ferrugineus* fail to develop in similar circumstances owing to their inability to enter the grains.

In general, fewer larvae were recovered than the total number of eggs added to each tube. Unhatched eggs were never found but those which failed to hatch may have been eaten by surviving larvae. As the total number unaccounted for in every case exceeded the average mortality found by Davies (1949) in his individual culture experiments, it is also possible that some viable eggs were eaten as well. If so, there was no apparent correlation between the adequacy of the diet and the number of eggs lost. Such correlation did, however, occur later in the life cycle where instances of cannibalism were noticed on the three least favourable foods. A total of five decapitated third- or fourth-stage larvae were found in tubes of National and Canadian flour and three dismembered adults in English wheat. There was, however, no evidence of first- and second-stage larvae attacking each other. In the case of National flour the total number of larvae unaccounted for rose considerably as the end of the life history approached, suggesting a higher degree of cannibalism than appeared likely from the number of dismembered larvae found. On the other hand, no such rise occurred on Canadian flour where the mortality figures were also high.

Lucas and Oxley (1946) record instances of cannibalism by adult *Laemophloeus* but do not attribute the same habit to the larvae. Rilett (1949) states that prepupae and pupae of *L. ferrugineus* may be attacked by younger instars if encountered in parts of wheat grains on which the latter wish to feed. It appears from the present observations that there is at least a tendency towards such behaviour in both larvae and adults when the food supply is unfavourable.

Feeding.

Lucas and Oxley (1946) stated that larvae of the species since named *L. pusilloides* feed exclusively on the germ when reared on Manitoba wheat. This fact was also noted in the case of *L. minutus* in the course of the present work but, in two instances, there were indications that the endosperm surrounding the germ of the softer English wheat had been attacked. There was evidence too, that the germ of more than one grain might be attacked by the same larva but only rarely.

Rilett (1949), in mentioning that the larvae of *L. ferrugineus* select the germ as a source of food, stated that feeding may on occasions take place on the endosperm but particularly in heavily infested grain where previous generations have already consumed the germ of a high proportion of grains. The duration of the life cycle is, however, longer in these circumstances and mortality is higher. He recorded, too, that at 30°C. and 75 per cent. R.H. a single germ is sufficient to carry a larva of *L. ferrugineus* through its full period of development, although it might not be adequate at low temperatures and humidities. The present work, therefore, indicates marked similarity between the preferences and requirements and *L. minutus* and *ferrugineus* during their development on wheat.

The observations produced slight evidence that the endosperm of English wheat may be attacked by adult *L. minutus*. Davies (1949) in observations on the mode of attack on wheat grains found that, in most grains damaged by *L. minutus*, the embryo was consumed although, occasionally, the endosperm alone was eaten. Rilett (1949) stated, however, that adult *L. ferrugineus* feed on damaged endosperm and wheat dust and makes no mention of the germ in this connection.

As regards broken maize there did not appear in the present work to be the same preference for the germ. Many larvae were found burrowing into pieces of germ, with perhaps two or three to one piece, but just as many were found at all stages to be free living amongst the broken pieces. It is possible that these obtained at least part of their food from powdered endosperm covering broken pieces of pericarp.

Sex Ratio.

The sex ratio figures show, on the whole, a preponderance of females but statistical treatment by means of the Chi-squared test indicates that only in the

TABLE III.

Sex ratio of *L. minutus* reared on various food media.

Food	Total ♂	Total ♀	Chi-squared	P
Manitoba wheat ..	113	115	0·018	0·9—0·8
English wheat ..	59	60	0·008	0·95—0·9
Plate maize	95	114	1·728	0·2—0·1
Wholemeal flour ..	126	124	0·016	0·9
National flour ..	22	42	6·260	0·02—0·01
Canadian flour ..	19	27	1·400	0·3—0·2
All combined	434	482	2·520	0·2—0·1

case of National flour, where a comparatively small number of adults emerged, did the ratio differ significantly from 1. When considering the total number of males and females which emerged on all foods, it is found that there is no significant difference between the sexes (Table III).

Cocoon Formation.

On both types of wheat, development of the majority of pupae took place within the cavities formed by consumption of the germ. In most cases the entire germ was eaten but in a few grains of English wheat a small portion remained alongside the cocoon and adhering to it. All frass was voided from the cavities before formation of the cocoon which sealed all breaks in the overlying pericarp and testa. A few larvae left the grains on completion of feeding to pupate on the bottom or sides of the tubes. Cocoons in such positions were protected by one or more wheat grains adhering to the exposed surface.

Similarly, in tubes of Plate maize, cocoons were formed on the base and sides of tubes. Others occurred between several broken pieces of pericarp linked together by the cocoon, in crevices in the broken pieces, or occasionally in cavities burrowed in the germ.

An interesting feature of the development of the species on the least suitable foods, National and Canadian flours, was the inability of a number of larvae which survived until late in the fourth instar to form cocoons. This contrasts sharply with the sequence of events on wholemeal flour where cocoons were formed either against the sides of the tubes, lying singly in the flour or in groups of two or three, stuck together or attached to each other by strings of webbing. Two cocoons, containing live pupae, found on this flour were perforated with holes but in all other cases the walls were complete.

On National and Canadian flours some normal cocoons developed in positions similar to those in wholemeal flour but not all the larvae which reached the stage of producing silk succeeded in forming more than a mass of loose webbing and failed to model a complete cocoon. Both prepupae and pupae occurred amongst such webbing and also in flour where there was no sign of webbing. Many of these died, as indeed did a number which developed within the normal cocoons produced. The recovery of a freshly emerged adult from a tube of Canadian flour suggests that pupae may succeed in completing the life cycle in these abnormal conditions. Four were also extracted from tubes of National flour and three from Canadian flour in Series I.

Discussion.

Fraenkel and Blewett (1943) found that a number of beetles, other than *Laemophloeus*, and moths which commonly infest wheat or flour developed as successfully on 85 per cent. extraction (National) flour as on wholemeal flour. Flours of lower extractions all provided less suitable diets for each species and were responsible, in every case, for lengthening the period of development and increasing mortality.

The results of the present studies are at variance with these findings in that National flour proved to be far inferior to wholemeal in providing an adequate diet for *L. minutus*, owing to the high mortality associated with it. The results agree in that a food medium of an extraction rate lower than 85 per cent., such as Canadian flour (75 per cent.), was less favourable than either wholemeal or National flours. The same workers also stated that when fed on whole wheat all seven species they studied consumed the germ although four of them also attacked the endosperm to varying degrees. Rilett (1949) made similar observations with *L. ferrugineus* and found that wheat bran was second to the germ in providing an adequate diet for the species although it doubled the period of larval development and greatly increased mortality. White flour, he noted, was inferior to both germ and bran and lengthened the life cycle and increased the death rate still further.

Poorer development on flours of extractions below 85 per cent. was attributed by Fraenkel and Blewett to a deficiency of B-complex vitamins, the percentage of which falls as the extraction rate is lowered (Thomas, Bina & Brown, 1942; Andrews, Boyd & Terry, 1942; Tepley, Strong & Elvehjem, 1942). The figures given by McCance and others (1945) for aneurin, riboflavin and nicotinic acid in wholemeal, National and Canadian flours illustrate this point clearly and are summarised in Table IV.

TABLE IV.

Constituents of Manitoba and English wheats, Plate maize, wholemeal, National and Canadian flours.

Food	gm./100gm.			Aneurin (I.U./gm.)	Riboflavin (μg./gm.)	Nicotinic acid (μg./gm.)
	Protein NX5·7	Fat	Carbohydrate (as starch)			
Manitoba wheat ..	13·62	2·49	63·0	1·18	1·7	55·0
English wheat	8·89	2·23	66·8	0·96	1·7	48·0
Wholemeal flour (Grist = 70% Man. 30% English wheat)	13·30	2·16	62·5	1·20	1·9	—
National flour ..	13·2	2·03	68·0	0·95	1·7	17·0
Canadian flour .. (75% extraction) ..	* 14·3	* 1·08	* 65·5	0·29	0·7	9·6
Plate maize	10%	4·3%	71·7%	1·40	1·3	7·0

* Figures given by analysis of actual flour used.

In recent years knowledge of the distribution of vitamins has increased considerably. Hinton (1944) stated that the scutellum fraction of the germ contains about 60 per cent. of the total aneurin in the wheat berry. Later, Moran (1945) recorded that the bran is particularly rich in nicotinic acid which also occurs to a marked degree in the outer endosperm. According to the same author, riboflavin is more uniformly distributed throughout the wheat grain but the highest concentration is in the germ. As the extraction rate of flour falls, the germ is eliminated and increasing amounts of scutellum, bran and outer endosperm are excluded, resulting in the steady reduction of B-group vitamins. It is clear from the above that dependence on a certain minimum content of members of the B-complex for optimum development could account for Rilett's results with *L. ferrugineus* mentioned above as well as those obtained by Fraenkel and Blewett with other species.

The work of McCance and others (1945) and Bacharach and Rendle (1946) on the normal constituents of the remaining foods used in the present work indicated considerable variation in the content of B-complex vitamins in the six materials, particularly as regards nicotinic acid. Figures for Plate maize are not available but Schwarz (1945) gave data on the constituents of American yellow corn and stated that the variation of Plate maize from published data on the maize of other countries was negligible.

From the figures given by these workers, as shown in Table IV, it would appear that a deficiency of nicotinic acid cannot be entirely responsible for poor development on Canadian and National flours as maize apparently has an even lower content than either. Again, the normal lack of B1 in Canadian flour should not contribute to the failure of this food in the present work as analysis of the particular commercial product employed gave a value of 0·83 i.u./gm., indicating that B1 had been added to bring its level more in line with that of higher extraction flours.

It would seem, therefore, that failures in the development of *L. minutus* are not caused entirely by deficiencies of any of the three B-complex vitamins mentioned. It is likely, however, that such deficiencies are largely contributory in determining which foods form suitable media for the species but lack of one may be compensated to some extent by excess of another. The same can probably be said of other members of the B-group which are lacking to some degree in National and Canadian flours but figures are not available to substantiate this suggestion.

Data from the same sources also indicate that there is a considerably lower mineral content in National and Canadian flours than in whole wheat, wholemeal flour or Plate maize, all of which agree fairly closely in this respect. Furthermore, the proportion of fat in Canadian flour is low and may well have fallen below the critical level for *L. minutus*. It is possible that both these factors play a part, if not as vital as vitamin content, at least of considerable importance in deciding the relative adequacy of individual diets for the species.

Summary.

Laemophloeus minutus (Ol.) has been reared on six food materials of a type with which the genus, *Laemophloeus*, is commonly associated in the field. Consideration of the length of egg to adult development, together with the mortality, recorded from each medium indicates that Manitoba wheat and wholemeal flour are equally favourable for the development of the species, followed in order of precedence by Plate maize, English wheat and, finally, National (85 per cent. extraction) and Canadian (70–75 per cent. extraction) flour which proved equally unfavourable.

The stage of the life-history at which mortality mainly occurred varied with the diet. The high death-rate on English wheat was caused by the inability of newly hatched larvae to enter grains undamaged in the germ region. Mortality on National and Canadian flour occurred chiefly in the fourth instar.

There were indications of cannibalism in both larval and adult stages, at any rate when the diet was unfavourable.

The germ of wheat was attacked in preference to any other part of the grain. Maize germ was also consumed but whether it was preferred to the same extent as that of wheat was not established.

Pupation was mainly, but not exclusively, intergranular in wheat. Normal cocoons were formed in National and Canadian flours but some larvae pupated in loose webbing or in flour free from webbing and freshly emerged adults were observed in unwebbed National and Canadian flour.

Acknowledgements.

This work was carried out under the direction of Prof. J. W. Munro at the Department of Zoology and Applied Entomology, Imperial College of Science and Technology, and is published by permission of the Ministry of Agriculture and Fisheries. I am greatly indebted to Prof. O. W. Richards and Mr. R. G. Davies of the former Department for their helpful advice and criticisms during the progress of the work.

Valuable assistance has also been received from Dr. J. A. Freeman of the Infestation Control Division, Ministry of Agriculture and Fisheries, and my thanks are also due to Dr. T. Moran and Mr. E. N. Greer of the Research Association of British Flour Millers, St. Albans, for analysis of the Canadian flour used in the experiments.

References.

Andrews, J. S., Boyd, H. M. & Terry, D. E. (1942). The riboflavin content of cereal grains and bread and its distribution in products of wheat milling.—Cereal Chem., **19**, pp. 55–63.

Bacharach, A. L. & Rendle, T. (1946). The nation's food. A survey of scientific data.—London, Soc. chem. Industr.

Davies, R. G. (1949). The biology of *Laemophloeus minutus* Oliv. (Col. Cucujidae).—Bull. ent. Res., **40**, pp. 63–82.

Fraenkel, G. & Blewett, M. (1943). The natural foods and the food requirements of several species of stored products insects.—Trans. R. ent. Soc. Lond., **93**, pp. 457–490.

Freeman, J. A. (1952). *Laemophloeus* spp. as major pests of stored grain.—Plant Path., **1**, pp. 69–76. 42

Hinton, J. C. (1944). The chemistry of wheat germ with particular reference to the scutellum.—Biochem. J., **38**, p. 214.

Howe, R. W. (1943). An investigation of the changes in a bin of stored wheat infested by insects.—Bull. ent. Res., **34**, pp. 145–158.

Lucas, C. E. & Oxley, T. A. (1946). Study of an infestation by *Laemophloeus* sp. (Coleoptera Cucujidae) in bulk wheat.—Ann. appl. Biol., **33**, pp. 289–293.

McCance, R. A., Widdowson, E. M., Moran, T., Pringle, W. J. S. & Macrae, T. F. (1945). The chemical composition of wheat and rye and of flours derived therefrom.—Biochem. J., **39**, pp. 213–222.

Moran, T. (1945). Nutrients in wheat endosperm.—Nature, Lond., **155**, pp. 205–206.

Oxley, T. A. & Howe, R. W. (1944). Factors influencing the course of an insect infestation in bulk wheat.—Ann. appl. Biol., **31**, pp. 76–80.

Reid, J. A. (1942). The species of *Laemophloeus* (Coleoptera: Cucujidae) occurring in stored foods in the British Isles.—Proc. R. ent. Soc. Lond., (A) **17**, pp. 27–33.

Rilett, R. O. (1949). The biology of *Laemophloeus ferrugineus* (Steph.).—Canad. J. Res., (D) **27**, pp. 112–148.

Schwarz, G. (1945). Nutrient contents of samples of Argentine corns.—Rev. Fac. Cienc. quím. La Plata, **20**, pp. 175–179. (Chem. Abstr., **42** p. 2028.)

STEEL, W. O. & HOWE, R. W. (1952). A new species of *Laemophloeus* (Col.: Cucujidae) associated with stored products.—Proc. R. ent. Soc. Lond., (B) **21,** pp. 86–88.

TEPLEY, L. J., STRONG, F. M. & ELVEHJEM, C. A. (1942). Nicotinic acid, pantothenic acid and pyridoxin in wheat and wheat products.—J. Nutr., **24,** pp. 167–174.

THOMAS, J. M., BINA, A. F. & BROWN, E. B. (1942). The nicotinic acid content of cereal products.—Cereal Chem., **19,** pp. 173–180.

TUKEY, J. W. (1943). Comparing individual means in the analysis of variance.—Biometrics, **5,** pp. 99–114.

OBSERVATIONS ON THE EFFECT OF EXPOSURE TO A LOW TEMPERATURE ON *LAEMOPHLOEUS MINUTUS* (OL.) (COL. CUCUJIDAE).

By Gwyneth C. Williams.
Ministry of Agriculture and Fisheries
Infestation Control Division.

Although the relative importance of the various species of *Laemophloeus* as pests of stored grain has yet to be established with certainty, they are known to occur commonly in infestations of wheat and many other stored products. It is desirable, therefore, to know whether representatives of individual species are capable of surviving the winter in unheated warehouses in Britain, thus forming a reservoir of infestation liable to attack infestible commodities stored during the following spring and summer. The only recorded evidence on the subject is that of Mansbridge (1936) who found that larvae of *L. turcicus* Grouv. survived a winter during which the temperature occasionally fell below 0°C. for periods up to a maximum of two days, whilst adults of the species died off, and of Howe (1943) who reports that *Laemophloeus* will survive the winter in bulk wheat in conditions which prove fatal to *Calandra* (Col. Curculionidae).

In spite of these indications that certain species can resist winter conditions in this country, no information exists on the " cold-death-point " nor the relative susceptibility of the various stages of the life cycle to low temperatures. The present work is confined to a study of the effects on each instar of varying periods of exposure to the same low temperature with consideration in certain cases of the influence of humidity on the reaction.

Owing to the discovery by Lucas and Oxley (1946) of another species closely resembling *L. minutus* (Ol.), since described by Steel and Howe (1952) as *L. pusilloides*, the genitalia of a large number of specimens from the stock cultures were examined to establish that the species used in the present investigations was in fact *minutus*. Without exception it was found that the structure of both male and female genitalia tallied exactly with that figured by Reid (1942) for *L. minutus.*

Method.

Specimens were exposed in batches of 50, placed in 2 × $\frac{7}{8}''$ glass tubes covered with bolting silk. Adults used during the experiments were drawn from cultures reared on wholemeal flour + 5 per cent. yeast in constant conditions of 28°C. and 75 per cent. R.H. and transferred to 25°C. and 75 per cent. R.H. about 10 days before the first tests were made. Supplies of eggs were obtained by placing a large number of adults on an oviposition medium of flour, previously passed through a 100-mesh sieve, which was seived again after 24 hours to recover eggs laid during that period.

trs.

Larvae and pupae were obtained from eggs laid at 25°C. and 75 per cent. R.H. and reared in the same conditions on a food medium of wholemeal flour + 5 per cent. yeast. All specimens used in any one experiment were drawn from the same culture in order to guard against possible variation in their susceptibility due to differences in nutrition.

A temperature of 2°C. was selected for the tests but, unfortunately, it proved impossible to maintain this level constantly in the refrigerator available. Fluctuations continually occurred between +0·5°C. and +2°C. and on three occasions the reading fell as low as $-0{\cdot}5$°C. for a short period. Variation in the relative humidity both in the refrigerator and at 25°C. was obtained by placing saturated solutions of potassium chloride, sodium chloride and magnesium chloride in desiccators to give 35, 75 and 88 per cent. R.H., respectively. (Janisch, 1933.)

After exposure, the insects were returned to 25°C. and the appropriate humidity for 12 hours or, in the case of eggs and pupae, until hatching had finished. In assessing mortality, only those specimens showing no activity were counted as dead. In every case there were a few showing slight movement which probably died later but these were not included in the mortality figures.

Statistical analysis.

Two types of experiment were planned. In some cases the design was such as to allow analysis of variance on percentage mortalities transformed to "angles of equal information." In other cases a method of calculating a "median lethal time" and a "susceptibility coefficient" were adopted. These were obtained by a modification of the procedure employed in insecticidal bioassay for comparing the toxicity of different chemical compounds (Bliss, 1935 *a* and *b*; Finney, 1947). The mortality occurring after any given period of exposure was found in preliminary trials to be related to exposure time in such a way that a linear relation occurred between log. exposure time and the probit function of mortality. By calculating the equation to such a regression line it was possible to determine the median lethal exposure time (LE 50)—defined as the exposure necessary to kill 50 per cent. of the insects—and the standard error of this quantity. Comparison of the susceptibility of different developmental stages or the effect of different pre-cooling treatments could then be made by comparison of regression lines. This method utilises all the data available over a whole range of exposure times and mortalities and provides a highly efficient method of comparison. Susceptibility coefficients could be estimated as the ratio of the appropriate LE 50's which themselves are the most accurate available measure of cold-resistance. A similar method was also used by Johnson (1940) in the analysis of mortality figures for eggs of *Cimex lectularius* L. exposed to a number of temperature and humidity combinations.

1. Experiments with Adults.

(a) Comparison of humidities.

(1) In a preliminary experiment, separate batches of males and females were exposed at 35, 75 and 88 per cent. R.H. for periods of 12, 24, 48, 96, 112 and 288 hours. All the tubes were placed in the refrigerator at 2°C. at the same time and one of each sex removed after the appropriate interval. Controls were kept on a small quantity of wholemeal flour at 25°C. and 75 per cent. R.H. As mortality of both sexes was 100 per cent. at 112 hours and 96 and 100 per cent. for females and males respectively at 96 hours, the longest exposure period used in subsequent experiments was 96 hours.

(2) In a second experiment batches of 50 adults, 25 male and 25 female, were exposed to 2°C. for periods of 24, 36, 48, 60, 72, 84 and 96 hours at the same humidities as before. Controls were kept, one on wholemeal flour at 25°C. and 75 per cent. R.H., and three without food at 25°C. and 35, 75 and 88 per cent. R.H. When correcting the final results only mortality in the set with food was taken into consideration.

Analysis of the results by the probit method indicated that difference in humidity had no significant effect on mortality. There was some variation in the LE 50 obtained at each humidity but the three values gave an average of $65{\cdot}8$ hours (Table I).

Further analyses by the same method using the separate figures for males

TABLE I.

Effect of varying humidity on mortality of *L. minutus* adults exposed to +2°C. (Expt. 1 (a)).

Exposure (hours)	Mortality % (corrected for control mortality)			Comparison of humidities			LE 50	
	35% R.H.	75% R.H.	88% R.H.	Humidities compared	T.	P.	R.H.	Hours
24	2·0	8·0	6·0	35 & 75	1·33	>0·1	35	63·3
36	14·0	12·0	20·0	35 & 88	0·96	>0·3	75	68·1
48	18·0	18·0	22·5	75 & 88	0·81	>0·4	88	65·9
60	48·9	36·8	41·3				Mean LE 50	65·8
72	66·7	50·0	66·7					
84	75·0	85·4	73·9					
96	95·6	79·2	87·5					

The number of specimens tested at each exposure consisted of 25♂ and 25♀.

and females showed that the male was significantly more susceptible to exposure to a low temperature than the female. Taking an average of the susceptibility coefficients obtained at the three humidities, males appear to be 1·21 times more susceptible than females (Table II).

TABLE II.

Influence of sex on response of *L. minutus* adults to exposure to +2°C. (Expt. 1 (a)). (Based on mortality figures given in Table I.)

R.H.	t.	P.	LE 50 (hours)		Susc. coeff. ± S.E.
			♂	♀	
35	2·45	<0·05	57·3	69·7	1·22 ± 0·39
75	2·63	<0·05	60·0	71·4	1·19 ± 0·15
88	2·38	<0·05	55·6	67·8	1·21 ± 0·24

(*b*) *Comparison of male and female.*

A single experiment was conducted at one humidity only, namely 75 per cent. R.H., confining males and females in separate groups of 50 and placing them in the refrigerator at 2°C. for periods of 12, 36, 48, 60, 72, 84, 96 and 108 hours. The same method of statistical analysis was used as before. Close agreement was obtained with the results outlined above. Males again proved more susceptible than females and a value of 1·22 was obtained for the susceptibility coefficient (Table III).

TABLE III.

Comparison of ♂ and ♀ mortality at 75 per cent. R.H. (Expt. 1 (b)).

Exposure (hours)	Mortality % (corrected for control mortality)		t	p	LE 50 (hours)		Susc. coeff. ± S.E.
	♂	♀			♂	♀	
12	0	0	2·91	0·02	52·9	64·5	1·22 ± 0·16
36	0	0					
48	2·0	0					
60	4·0	8·0					
72	8·0	8·0					
84	28·0	10·0					
96	50·0	20·0					
108	72·0	36·0					

(c) Effects of previous starvation.

Batches of 25 males and 25 females were starved for periods of 12, 24 and 48 hours before being placed in the refrigerator at 2°C. and 75 per cent. R.H. for 60 hours, using five replicates in each case. The first of two sets of controls kept at 25°C. and 75 per cent. R.H. were starved for the same periods as those to be exposed to the low temperatures before being placed on wholemeal flour whilst a second was kept on wholemeal flour, without previous starvation, for the total

TABLE IV.

Effect of previous starvation on mortality of *L. minutus* adults exposed to +2°C. for 60 hours (Expt. 1 (c)).

Sex	Mortality % (Corrected for control mortality)			Source of variation	F.	P.	Average mortality of all replicates	Degrees Inverse sine transformation
	48 hours previous starvation	24 hours previous starvation	12 hours previous starvation					
♂	68·2 54·5 68·2 59·1 59·1	61·9 52·6 66·7 81·0 95·2	50·0 61·5 75·0 54·8 70·8	previous starvation	2·48	0·2—0·1	♂65·2	54·03
♀	24·5 28·6 24·5 57·1 57·1	52·0 80·0 44·0 44·0 32·5	41·7 41·7 33·3 37·5 29·5	Sex	24·52	<0·001	♀41·8	40·20
							Least significant interval (P=0·05)	7·02

period of the experiment. Mortality in the latter only was taken into consideration when correcting the experimental figures for statistical treatment. By examination of the results by an analysis of variance, it was found that previous starvation did not significantly influence the reaction to cooling but that a significant difference existed between the sexes, the males again being more susceptible than the females (Table IV).

2. Experiments with Eggs.

Comparison of humidities.

In a preliminary experiment, exposing groups of 50 eggs to a temperature of 2°C. for periods of 12, 24, 48, 96 and 192 hours at 35, 75 and 88 per cent. R.H., it was found that no eggs hatched at any humidity after the longest exposure period and that only two hatched after 96 hours at 88 per cent. R.H. An upper limit of 84 hours was, therefore, fixed for a more detailed experiment in which exposure periods of 6, 12, 24, 48, 72 and 84 hours at 2°C. were used at the same three humidities. A control was kept at 25°C. and 75 per cent. R.H. By analysis of the results by the probit method it was again found that differences in the relative humidity made no significant difference to mortality. The LE 50's at the three humidities gave a mean value of 25·1 hours (Table V).

TABLE V.

Effect of varying humidity on mortality of *L. minutus* eggs exposed to +2°C. (Expt. 2).

Exposure (hours)	Mortality % (corrected for control mortality)			Comparison of humidities			LE 50	
	35%R.H.	75%R.H.	88%R.H.	Humidities compared	t.	P.	R.H.	Hours
6	20·5	2·3	4·5	35 & 75	0·85	>0·3	35	27·7
12	23·3	34·1	29·5	35 & 88	0·19	>0·9	75	23·4
24	38·6	40·9	34·1	75 & 88	0·65	>0·5	88	24·3
48	75·0	72·7	72·7				Mean LE 50	25·1
72	77·3	86·4	90·9					
84	88·6	95·5	93·3					

3. Experiments with Larvae.

Three replicates of the first, second, third and fourth instars, each containing 50 larvae, were all placed in the refrigerator at the same time and left for 60 hours at 2°C. and 75 per cent. R.H. Two controls for each stage were kept at 25°C. and 75 per cent. R.H., one on a small quantity of wholemeal flour, previously passed through an 80 mesh sieve to remove the coarser particles, and one without food. Mortality in the starved controls was so high that only the death rate of those with food was considered in the correction of the final results which are summarised in Table VI. By an analysis of variance, it was found that fourth instar larvae are less susceptible to cooling to 2°C. than the other three which form a group in which there is no significant difference between the stages in their reaction to exposure to the same temperature.

TABLE VI.

Effect of 60 hours exposure to +2°C. on larval instars of *L. minutus* (Expt. 3).

Instar	Mortality % (corrected for control mortality)	Mortality % (average of replicates)	Degrees. Inverse Sine transformation
1st	14·9 29·8 27·7	24·1	29·30
2nd	68·0 36·0 56·0	53·3	49·97
3rd	66·7 71·8 56·2	68·2	53·80
4th	0 7·0 0	2·3	5·10
		Least significant interval (P=0·05)	23·67

Horizontal lines in last column separate groups differing significantly from each other but not within themselves.

4. Experiments with Pupae.

Groups of 50 unhatched cocoons were placed in the refrigerator at 2°C. and 75 per cent. R.H. for periods of 12, 24, 48 and 96 hours with a control kept at 25°C. and 75 per cent. R.H. After removal from the cold environment the cocoons were examined at intervals of 12 hours and adults were removed as they emerged. The results indicated that a high proportion of pupae may survive at least 96 hours exposure without ill effect but the number of observations were insufficient to allow statistical analysis.

5. Experiments with all Stages.

The experiment was set up using two replicates of 50 specimens of each stage, including eggs, and tubes containing 25 males and 25 females of the parent generation from which all the other stages were reared. These were all placed in the refrigerator at the same time and left undisturbed for 60 hours at 2°C. and 70 per cent. R.H. A control for each instar was kept at 25°C. and 75 per cent. R.H. with larvae and adults on a small quantity of flour previously passed through an 80 mesh sieve.

By an analysis of variance it was found that the seven stages of the life cycle fall into three groups, differing significantly from one another, but not within themselves, in their reaction to cold. It is seen thus that pupae in their cocoons and fourth-instar larvae are more resistant than any of the other stages, followed by the first, second and third instars and adults which, in their turn, are more resistant than eggs (Table VII).

The results of previous experiments in which fourth-instar larvae were less susceptible than those of earlier instars and LE 50's of 65·8 and 25·1 hours respectively indicated that adults have greater resistance than eggs to the same low temperature, are thus borne out. It was also observed during this experiment that surviving larvae of all stages will eventually pupate normally if kept on wholemeal flour at 25°C. and 75 per cent. R.H.

TABLE VII.

Effect of 60 hours exposure to +2°C. on all stages of *L. minutus* (Expt. 5).

Instar	Mortality % (corrected for control mortality)	Mortality % (average of replicates)	Degrees. Inverse Sine transformation	Significantly differing groups
Adult ..	26·0 26·0	26·0	30·70	Egg 52·25
Pupa ..	2·0 2·0	2·0	8·10	LI 38·25
4th ..	6·0 8·0	7·0	15·30	Adult 30·70
3rd ..	20·8 18·7	19·8	28·65	L2 28·65
2nd ..	12·5 18·7	15·6	22·75	L3 22·75
1st ..	37·5 39·2	38·4	38·25	L4 15·30
Egg ..	58·3 66·7	62·5	52·25	Pupa 8·10
		Least significant interval (P=0·05)	9·19	

Horizontal lines in last column separate groups differing significantly from one another but not within themselves.

Discussion.

The cold-hardiness of insects, which varies widely with the species, is influenced by a number of factors and is largely linked with the biophysics of metabolic water in living organisms. Imms (1937, pp. 220–227), in discussing this point, reviewed work which indicated that much of the water in a cold-hardy species is bound or adsorbed in such a way that it only freezes at a comparatively very low temperature. Provided the temperature is lowered slowly the proportion of water held in this way increases as the temperature falls below freezing point and the ratio of "bound" to free water, if high enough, acts as a protection against freezing temperatures.

Sacharov (1930) considered that cold-hardiness depends not only on the proportion of free water which can freeze easily but also on the fat content of the body. The latter point is borne out by the results of the foregoing experiments where the male proved to be less resistant than the female which would be expected to contain a higher percentage of fat. No conclusions can be reached as to differences in the relative susceptibility of the various larval instars although, again, the least susceptible fourth stage probably has the highest fat content.

Payne (1929) stated that cold-hardiness is inversely proportional to both relative and absolute humidities regardless of the temperature and quotes figures to show that freezing and undercooling points of larvae of the beetle *Synchroa punctata* Newm. are greatly lowered by desiccation. In the present studies, however, variation in the relative humidity had no significant effect on the survival of, at least, eggs and adults. Johnson (1940) found that at temperatures above and below 13°C., the developmental-hatching threshold for the species, humidity had a slight but definite effect on the survival of *Cimex lectularius* eggs. He also records slight but definite evidence that, at 4 and 12°C., relative humidities between 50 and 80 per cent. may be more favourable than those higher and lower in the scale but is of the opinion that there is no obvious, simple relationship between humidity and survival over a wide range of temperatures.

Of other topics discussed in the present work, the observation that previous starvation has no effect on the survival of *L. minutus* adults submitted to cooling does not bear out the results of other authors. Payne (1929), amplified by Sacharov (1930) found greater resistance to cold in starved insects.

Mellanby (1939), following observations on a number of species, stated that cold-hardiness is influenced considerably by the temperature to which insects are acclimatised before exposure to cold, specimens from warm conditions being killed more easily at temperatures below zero than members of the same species from a cooler environment. In the present work, all specimens had lived before chilling at the same temperature, 25°C., for considerably longer than the 20 hours found by Mellanby to be necessary for acclimatisation to a given temperature and different results might be expected in experiments where another pre-cooling temperature was used. The results given above indicate that *L. minutus* can survive in conditions where the temperature only falls as low as 2°C. for short periods with a maximum of about four days. The temperature to which specimens in unheated food stores, not associated with hot spots in grain, are exposed normally falls gradually during the autumn so that the insects are usually acclimatised to an environment considerably cooler than 25°C. by the beginning of the winter. As a consequence, *L. minutus* may endure sudden exposure to 2°C. and lower more readily in the field than appears from the experiments described. It seems, in fact, that the species can probably survive a normal winter in warehouse conditions in this country but may be killed off by an abnormally cold season.

Summary.

Experiment showed that all developmental stages of *Laemophloeus minutus* (Ol.) can survive exposure to a temperature of + 2°C. for a limited period which varies with the instar.

The egg was more susceptible to such exposure than any other stage, followed by the first, second and third larval instars and the adult, which did not differ significantly from each other, and then by the fourth-instar larva and pupa which can also be grouped together.

The adult male proved 1·21 times more susceptible than the female to the effects of exposure.

Atmospheric humidity did not influence the mortality of eggs or adults. Previous starvation did not affect the mortality of adults subsequently exposed to + 2°C.

Acknowledgements.

This work was carried out under the direction of Prof. J. W. Munro at the Department of Zoology and Applied Entomology, Imperial College of Science and Technology, and is published by permission of the Ministry of Agriculture and Fisheries. I am greatly indebted to Prof. O. W. Richards and Mr. R. G. Davies of the former Department for their helpful advice and criticisms during the progress of the work. Valuable assistance has also been received from Dr. J. A. Freeman of the latter organisation.

References.

Bliss, C. I. (1935*a*). The calculation of the dosage-mortality curve.—Ann. appl. Biol., **22,** pp. 134–167.

Bliss, C. I. (1935*b*). The comparison of dosage-mortality data.—Ann. appl. Biol., **22,** pp. 307–333.

Davies, R. G. (1949). The biology of *Laemophloeus minutus* (Oliv.) (Col. Cucujidae).—Bull. ent. Res., **40,** pp. 63–82.

Finney, D. J. (1947). Probit analysis.—256 pp. London, Cambridge Univ. Press.

Howe, R. W. (1943). An investigation of the changes in a bin of stored wheat infested by insects.—Bull. ent. Res., **34,** pp. 145–158.

Imms, A. D. (1937). Recent advances in entomology.—2nd edn., 431 pp. London, Churchill.

Janisch, E. (1933). Über die Methoden zur Konstanthaltung von Temperatur und Luftfeuchtigkeit im biologischen Laboratiumsversuch. Hanb. biol. Arb. Meth., **5,** pp. 87–112.

Johnson, C. G. (1940). Development, hatching and mortality of the eggs of *Cimex lectularius* L. (Hemiptera) in relation to climate, with observations on the effects of preconditioning to temperature.—Parasitology, **32,** pp. 127–173.

Lucas, C. E. & Oxley, T. A. (1946). Study of an infestation by *Laemophloeus* sp. (Coleoptera Cucujidae) in bulk wheat.—Ann. appl. Biol., **33,** pp. 289–293.

Mansbridge, G. H. (1936). A note on the resistance to prolonged cold of some insect pests of stored products.—Proc. R. ent. Soc. Lond., (A) **11,** pp. 83–86.

Mellanby, K. (1939). Low temperature and insect activity.—Proc. roy. Soc., (B) **127,** pp. 473–487.

Payne, N. M. (1929). Absolute humidity as a factor in insect cold-hardiness with a note on the effect of nutrition on cold-hardiness.—Ann. ent. Soc. Amer., **22,** pp. 601–620. 18 166

Reid, J. A. (1942). The species of *Laemophloeus* (Coleoptera: Cucujidae) occurring in stored foods in the British Isles.—Proc. R. ent. Soc. Lond., (A) **17,** pp. 27–33.

Sacharov [Sakharov], N. L. (1930). Studies on cold resistance in insects.—Ecology, **11,** pp. 505–517. 17 12

Steel, W. O. & Howe, R. W. (1952). A new species of *Laemophloeus* (Col.: Cucujjidae) associated with stored products.—Proc. R. ent. Soc. Lond., (B) **21,** pp. 86–88.

STUDIES OF HOUSE LEAVING AND OUTSIDE RESTING OF *ANOPHELES GAMBIAE* GILES AND *ANOPHELES FUNESTUS* GILES IN EAST AFRICA.

I.—THE OUTSIDE RESTING POPULATION.

By M. T. Gillies.
East African Malaria Unit, Amani, Tanganyika.

(Plate XXXII.)

While much recent research on the control of Anopheline mosquitos in Africa has been devoted to the development of effective formulations of residual insecticides, it is clear that exact studies on the behaviour of the principal vectors under natural conditions must continue to be of value. Of particular interest is the relationship of the mosquito to houses and the importance of these as resting places. A great deal of work on this aspect of the behaviour of *Anopheles gambiae* Giles and *A. funestus* Giles has been published in different countries over many years. The knowledge gained on the entry and biting activity of both species is detailed, and substantial agreement between workers in different countries has been achieved (Holstein, 1952). On the other hand, the results of studies on house resting and outside resting are sometimes conflicting, and in no case has attention been paid to more than one or two aspects of the problem in the same locality.

The value of studies in outside resting of *Anopheles* has been shown by recent work in several parts of the world. The methods employed have included direct searching in Malaya, by Wharton (1950), and in Trinidad, by Senior White (1951), the use of portable net traps lowered over vegetation on the savannahs of Colombia by De Zulueta (1950, 1952), or the digging of small pits in the ground in Africa by Muirhead Thomson (1951*b*).

In the past, observations in various inland regions of Africa have shown that *gambiae* adults may be caught resting outside, *e.g.*, Leeson (1931) in Southern Rhodesia, De Meillon (1934*a*) in the Transvaal, Symes (1941) in the highlands of Kenya, and Holstein (1952) in the Haute-Volta region of West Africa. Similarly, on the East African coast Muirhead Thomson (1951*b*) found fresh-water *gambiae* and *funestus* in outside harbourages. Records of *gambiae* caught outside in other coastal regions may refer to salt-water forms, which show distinct differences in regard to house resting, as shown on both the East and West African coasts (Muirhead Thomson, 1948).

In contrast to these findings Hocking and MacInnes (1948), working at Taveta on the Kenya-Tanganyika border, concluded that no *gambiae* or *funestus* were resting outside except when newly emerged, or immediately before or after egg-laying. Wiseman and others (1939), in many searches round Mombasa, found only three *gambiae* females resting outside.

In order to obtain a clearer picture of this phase of activity, a study was made of the pattern of resting in, and the exodus from, houses by females at all stages of the gonotrophic cycle in one particular area of Tanganyika. The results of this work are reported separately (Gillies, 1954), the present paper being devoted to the results of observations on the outside resting population.

This work was carried out over a period of twenty months in a small village 27 miles inland from the coastal town of Tanga and at an altitude of just over

600 feet. This village of Tengeni is 2½ miles from the field laboratory at Muheza, where meteorological records are kept and much of the sorting and dissection of material was carried out. The mean monthly temperature varied from 73°F. in July to 81·4°F. in March. Rainfall in 1951, an abnormally wet year, was 62·2 inches, associated mainly with the changes from the north-east to the south-west monsoon and back again, in April to May and October to December, respectively. There is therefore a long cool dry season (June to September) and a shorter hot one (January to March).

The country round Tengeni is typical of the foothills of the eastern Usambaras, as described by Wilson (1936). It is broken up by little hills and shallow valleys with overgrown streams and patches of swamp that hold water for the greater part of the year. The land is mostly under cultivation, maize and cassava being interspersed with tracts of fallow land covered with tall grasses, and scattered mango trees and coconut palms. Rice is grown on a small scale in some of the valleys, and these fields are flooded for a varying period after heavy rain. Only scattered stretches of riverine thicket remain along the streams, but there is evidently sufficient infiltration of tsetse flies into the area to preclude the keeping of cattle. The people, mostly of the Bondei tribe, live in rectangular mud-walled huts with roofs of palm thatch. These vary considerably in their state of repair, and in the numbers of openings they present for the entry and egress of mosquitos. Only one household in ten keeps sheep or goats, and these usually sleep in a separate portion of the same house.

Classification of Catches.

All mosquitos caught were examined without delay and classified according to the ovarian stages of Christophers. After a little experience, external appearances were used as a guide to the ovarian stages, but all doubtful cases and many obvious specimens were still dissected. In this respect the diagrams given by Hocking and MacInnes (1948) were found to be useful.

Further classification was made in the case of females with ovaries in Stage II, based on the degree of digestion of the blood. This group includes females in three quite separate phases of activity, which should be carefully distinguished, namely: those that have recently fed and whose stomachs contain fresh blood, those with partly digested old blood that have fed 24 to 36 hours previously, and those that are unfed. In the Tables that accompany this paper the following categories are used:

(1) " Unfed ", including virgin females with Stage I ovaries and unfed multiparous females with Stage II ovaries.

(2) " Fed ", including those with ovaries in Stages II and III and with fresh blood.

(3) " Gravid ", including those with ovaries in Stages IV and V, with partly or completely digested blood, and females with ovaries in Stage II, but containing blood in the degree of digestion usually associated with Stage IV or V eggs. The " Fed " group, therefore, are those caught on the morning following the taking of a blood meal, while the " Gravid " group are those caught on the second or third day after feeding.

If this method of grouping is adopted in an area where the gonotrophic cycle is longer than two days, some confusion may arise over those females with Stage III ovaries. This may be overcome by adopting the further subdivision of Stage III used by Macan (1950). He defined " Early Stage III " as having follicles in which the yolk granules occupy just more than half; " Stage III " in which the yolk granules occupy two-thirds; and " Late Stage III " in which the yolk occupies the whole egg and elongation has started. When the cycle lasts three days, on the first morning after feeding, the ovaries will be in Stage II or at the most Early Stage III. By the second morning they will mostly be in Late

Stage III or Stage IV, though a few may be at Stage III. By the third morning the ovaries will be at Stages IV or V. It is, of course, essential to verify this conclusion by observations on specimens that have fed at known times. In this paper females with Late Stage III ovaries have been classified with Stage IV for purposes of clarity.

Where the gonotrophic cycle lasts only two days no such difficulties arise, and the straightforward division of females into "Fed" and "Gravid" categories, as figured by Muirhead Thomson (1951*a*) can be applied.

Methods.

Natural outside resting sites.

Muirhead Thomson (1951*a*) has pointed out the difficulties encountered in and meagre results to be expected from direct searching for outside resting places. Even where a particularly productive natural shelter is found, the objection can be raised that observations made on a single shelter may not be representative of the outside population as a whole. Nevertheless, the method is of considerable value in checking the validity of samples collected by less direct methods, and in the course of the present investigations many hours were spent in collecting the small numbers found in natural sites, which are recorded in Table I.

Favourable resting sites for females were always marked by a double layer of shade. Thus there was always high shade from trees or overhanging bushes, while the actual resting places were again in the most sheltered possible position, under the overhanging edge of an earth bank or in depressions at the base of trees or the undersides of rocks (see Pl. XXXII, figs. 4, 5). The inaccessibility of these resting sites is in marked contrast to those of certain other species, for example *A. machardyi* Edw. or *A. demeilloni* Evans in the rain forest of the eastern Usambaras round Amani, which may be caught resting openly on tree trunks at any hour of the day.

Construction and use of artificial shelters.

As long ago as 1908, Blin in Dahomey described the use of "hole-traps" (trous-pièges), small tunnels dug in the ground, in which he found Anophelines and which he believed could be used as a means of control. Muirhead Thomson (1951*b*) dug little horizontal pits in earth banks, in which resting female Anophelines could conveniently be caught. In the Philippines, Russell and Santiago (1934) constructed an earth-lined box trap, in which the earth walls were kept constantly damp by a drip can and the front partially closed by a removable curtain. In the present investigation this type of artificial shelter was taken as a model and, after a little experimentation, a satisfactory box shelter was designed.

This consisted of a wooden frame, 3 ft. long by 3 ft. deep by 2 ft. wide, over which plastic gauze was stretched. The box so formed was buried in a suitable earth bank and the entrance partly covered with a black curtain, leaving below it a 6- to 8-inch gap for the entry of mosquitos (see Pl. XXXII). This provided a dark, virtually earth-lined, chamber and, after raising the curtain in the morning, the mosquitos resting in it could be easily caught by hand. It was found that the catches were far more affected by the siting of the shelters than by their construction. The amount of shade or the height of the vegetation round them, their conspicuousness or the proximity of houses, all seemed to influence the catches.

Daily hand-catching with test tubes was carried out six days a week during the periods of investigation. Males were caught in fair numbers, but the weekly average catch of females per shelter varied from 0·3 to 3 female Anophelines per day, although catches of up to 20 females in a single shelter were recorded on isolated occasions.

As this investigation was complementary to those being made at the same time on the house population, and time and man-power were therefore limited, a maximum of ten shelters was used. In this number is included a single large tunnel, 3 ft. square and 6 ft. deep, that was dug in the side of a heavily shaded river bank. These shelters were disposed so that four were within 20 yards of houses, while six were 200 yards or more away on the opposite side of a shallow depression and in or beyond the banks of a stream. A certain number of catches on the same lines were also made in the first two seasons, from another village two miles from Tengeni.

Outside Catches.

Results.

In Table I are set out the results of all outside catches. These figures show that the composition of catches made in three separate seasons was generally similar, and that the small sample of the *gambiae* population caught in natural sites does not differ in any important respect from the catches made in artificial shelters. The catches of *funestus* from natural sites, made as they were mainly during the hot season when the outside population is at a minimum, indicate a higher proportion of unfed females than catches from box shelters. The rainfall during the 1952 season was exceptionally low; this may account for the

TABLE I.

Outside catches from artificial shelters and natural sites.

A. gambiae

Season	No. of shelters	Total female	Unfed		Fed		Gravid	
			Nos.	%	Nos.	%	Nos.	%
Apr.–Aug./51	6	239	93	39	19	8	127	53
Oct.–Dec./51	5	186	70	38	12	6·5	104	55·5
Apr.–July/52	10	160	24	15	13	8	123	77
Natural sites Apr./51–July/52	—	55	22	40	4	7	29	53
Total	—	640	—	32·7	—	7·5	—	59·8

A. funestus

Season	No. of shelters	Total female	Unfed Nos.	Unfed %	Fed Nos.	Fed %	Gravid Nos.	Gravid %
Apr.–Aug./51	6	182	80	44	3	1·5	99	54·5
Oct.–Dec./51	5	230	109	47·5	13	5·5	108	47
Apr.–July/52	10	855	322	37·5	74	8·5	459	54
Natural sites Apr./51–July/52	—	70	56	80	2	3	12	17
Total	—	1337	—	42·4	—	6·9	—	50·7

low and high percentage of unfed and gravid *gambiae*, respectively, during that period.

In Table II it is seen that the ratio of fed to gravid *gambiae* varied from 1:4·6 to 1:12·5 according to siting, with an average of 1:8. It has been shown (Gillies, 1953) that in the low-lying coastal region the gonotrophic cycle lasts two days for all except the coolest few weeks of the year. Under these conditions, the fed and gravid categories represent the first and second days, respectively, of the gonotrophic cycle. These catches therefore are consistent with the view that few *gambiae* females leave houses immediately after feeding, or rest outside after biting in the open, but that many may do so during the second half of the cycle.

TABLE II.

Composition of catches in relation to siting of shelters.

	A. gambiae				*A. funestus*			
Distance from houses ..	Less than 200 yd.		More than 200 yd.		Less than 200 yd.		More than 200 yd.	
	Fed	Gravid	Fed	Gravid	Fed	Gravid	Fed	Gravid
Numbers ..	25	116	19	238	84	442	6	224
Ratio	1	4·6	1	12·5	1	5·3	1	37·3

The catches of *funestus* show a general similarity to those of *gambiae*, but it is noticeable that fed females are even more rarely caught outside except in the vicinity of houses. A further difference should be recorded. For six months of the year the mean temperature is below 78°F., during which period the gonotrophic cycle for a part, or all, of the *funestus* population lasts three days (Gillies, 1953), and a concomitant rise in the number of half-gravid and gravid females should then be apparent. The seasonal changes in the *funestus* catches, shown in Table III, are seen to reflect this increase. The hot season in this Table comprises those months of the year, mid-November to mid-May, when the mean monthly temperature is above 78°F.

TABLE III.

Catches of *A. funestus* in outside shelters.

Siting of shelters	Hot season			Cool season		
	Gravid	Total	% gravid	Gravid	Total	% gravid
Distant	67	219	30·6	157	277	56·7
Near	88	164	53·7	354	607	58·3
Total	155	383	40·5	511	884	57·8

The validity of catches in artificial outside shelters.

The use of artificial shelters is based on the assumption that they are competing with natural outside resting places, and act as an inducement to the mosquito population to adopt more accessible harbourages. Some evidence for this was noted on one occasion when a box shelter, set up in the vicinity of a known natural resting site remote from houses, appeared to " draw off " that particular section of the outside population during the week in which it was in position. The method should therefore be invaluable in studying Anophelines that are normally exophilic.

When applied to the investigation of the outside resting section of a species that is known to be predominantly house dwelling, the method has certain limitations, and should not be used without qualification. The disadvantage lies in the possibility that the artificial shelters may be competing with houses, and that mosquitos caught in them merely represent those that were abroad at night and might, in their absence, have re-entered houses at dawn. Where artificial shelters are set up at some distance from houses, say 200 yards in well vegetated country, this possibility seems remote. But where they are used in the vicinity of houses, the value of results obtained from them is less certain.

The validity of the catches recorded above may be tested by comparing the catches of *funestus* made in the hot (two-day cycle) and cool (three-day cycle) seasons, when, in the whole population, the ratio of fed to gravid must increase from 1 : 1 to 1 : 2.

The results of house catches, which will be described in the second paper in this series (Gillies, 1954), show that there is little seasonal change in the numbers of half-gravid and gravid females resting in houses and that, as a consequence, it would be expected that the numbers resting outside would be doubled in the cool season.

If the catches for all box shelters are taken together (Table III), it is seen that the proportion of gravid females outside increased from 40·5 to 57·8 per cent. with the change of the season, which, in fact corresponds almost exactly to a doubling of the numbers of gravid females caught outside, as the following calculation shows: $\frac{40{\cdot}5 \times 2}{100 + 40{\cdot}5} \times 100 = 57{\cdot}6$. At first sight this appears to afford substantial support for the validity of catches made in these shelters, but it should be noticed that there are marked differences between the catches made in distant shelters and in those near houses (P for this difference $<0{\cdot}01$). The seasonal change in the latter group is very slight, and strongly suggests that these shelters merely reflect the changes in the house resting population and that catches made in them are not wholly representative of the true outside resting population.

It may be concluded that the use of artificial shelters gives valuable information on the composition of the outside resting population, but that those set up near

TABLE IV.

Species composition of catches in relation to siting.

	A. gambiae		*A. funestus*	
	Distant	Near	Distant	Near
Unfed ..	147	40	266	245
Fed and gravid	257	141	230	526
Total ..	404	181	496	771
Percentage ..	69·1	30·9	39·1	60·9

houses cannot be relied upon to give a valid sample. Additional support for this view is provided by the catching of small numbers of normally exophilic species, *A. coustani* Lav., *A. marshalli* Theo., *A. nili* Theo. and some of the other members of the *funestus* group, in these distant shelters.

From the data given in Table IV it is seen that the majority of *gambiae* were caught in distant shelters, whereas 60 per cent. of the *funestus* were collected from shelters near houses. This proportion of the *funestus* catches, and rather less than one third of the *gambiae* catches, cannot therefore be accepted as material from which to draw valid conclusions on the composition of the outside resting population. Nevertheless, no investigation of outside resting would be complete without some observations on shelters adjacent to or within villages. Moreover, the results are of value in demonstrating the paucity of fed females to be found in a variety of outside situations.

Results of precipitin tests.

The stomach contents of the small numbers of recently fed specimens caught outside were submitted to precipitin tests to determine the source of the last meal. The stomach smears were tested with anti-sera prepared against man, monkey, dog, cat and sheep or goat. A few smears were taken from females in which a considerable degree of digestion of the blood had taken place. A large proportion of these gave negative results, and all of them have been omitted from the results shown in Table V.

TABLE V.

Results of precipitin tests on outside catches.

	Outside shelters			Empty house	
	Man	Dog	Negative	Man	Negative
A. gambiae ...	31	—	—	3	—
A. funestus ..	68	2	3	6	—

As shown above, the majority of fed specimens came from artificial shelters near houses, where the probability that they will have fed on man is high. The figures in the Table confirm this. But of those positive for man, twelve *gambiae* and five *funestus* were caught in distant or natural shelters. Despite the scantiness of the material on which to base conclusions, it appears significant that no *gambiae* were negative for man in any situation, and that the only *funestus* negative for man came from shelters near houses.

These results show no deviation from the man-biting habit on the part of females caught resting outside, and provide no evidence for supposing that any appreciable section of the population of either species is living away from man. This is very much what would be expected in an area where cattle are absent, other domestic animals are few, and wild animals of negligible importance.

Identity of funestus *females caught outside.*

As pointed out by other workers (De Meillon, 1936; Muirhead Thomson, 1951*b*), confusion with the vector species of other members of the *funestus* group that are not known to enter houses, *rivulorum* Leeson and *leesoni* Evans, can arise when females from outside resting sites are being studied.

In the early stages of this investigation no satisfactory method of separation was found except that all females with a pre-accessory dark spot or a second pale area in the upper branch of the 5th vein were excluded from the catches labelled as *funestus*. Early in the third season, however, two specimens of *rivulorum* and one of *leesoni* were caught biting man outside at dawn at Tengeni, and 4th-stage larvae were subsequently reared from the eggs they laid. This provided the necessary personal confirmation of the very clear differences between the eggs of these two species and *funestus* observed by earlier workers (De Meillon, 1934*b* and 1947; Evans & Leeson, 1935; Evans & Garnham, 1936).

Egg batches from 52 specimens of "*funestus*" caught in artificial outside shelters both near and distant from houses, and two specimens from natural sites, were all found to be typical of the vector species. The assumption that nearly all specimens caught were in fact *funestus* therefore seems to be justified.

Time of entry into outside shelters.

Observations in an unoccupied house had shown that the adoption of the final resting site for the day was by no means confined to the period between first light and sunrise and, accordingly, a limited number of observations were made on the time of entry of Anophelines into artificial shelters.

On 34 days, catches were made in two shelters twice in the course of each morning, at 07.00 and 11.00 hours. One shelter was in a relatively exposed position, the other in a more shaded spot. The results are shown in Table VI.

TABLE VI.

Composition of 34 early morning and late morning catches.

	Early			Late			Shaded shelter		Exposed shelter	
	Males	Females	Both	Males	Females	Both	Early	Late	Early	Late
A. gambiae ..	32	32	64	11	11	22	21	14	43	8
A. funestus ..	41	17	58	12	29	41	7	24	51	17
Total ..	73	49	122	23	40	63	28	38	94	25

It is seen that one-third of all Anophelines entered shelters after 07.00 hours and that *funestus* females tended to move in later than males and later than *gambiae* females. In the shaded site more than half had entered during the mid-morning period, whereas in the exposed shelter 79 per cent. were in place by the time of the first catch.

Although the numbers caught are very small they indicate the difference in the behaviour of the females of the two species under identical conditions (P for this difference $<0{\cdot}01$). These findings are also in general agreement with those of Eyles and Bishop (1943), who concluded that entry of *A. quadrimaculatus* Say in North America was a gradual process, earlier and more rapid where the daytime shelter under observation was in an exposed position.

Screening of outside shelters by houses.

In the course of building an experimental hut, opportunity was taken to observe the effect of this on catches made in a nearby artificial shelter. The hut was built ten yards from a box shelter and well to one side of it. Records of catches made in this and another shelter 200 yards away, before and after the putting up of the walls and roof of the hut, are set out in Table VII.

There was a striking fall in the numbers of both species caught in the adjacent shelter after the building of the hut. This must be attributed to the considerably larger number of presumably attractive openings presented to mosquitos seeking shelter in its immediate vicinity at dawn. It seems clear that the number of accessible houses in an area relative to the number of natural shaded harbourages must influence the proportion of mosquitos resting outside in the later stages of the gonotrophic cycle.

TABLE VII.

Effect of empty house on catches in adjacent shelter.

		Adjacent shelter			Distant shelter		
	Number of catches	*A. gambiae*	*A. funestus*	Both	*A. gambiae*	*A. funestus*	Both
9th Nov.–8th Dec. ..	25	46	33	79	78	82	160
House built from 9th–12th Dec.							
13th Dec.–19th Jan.	25	1	8	9	19	191	210

Outside Biting Activity.

In the foregoing sections the outside resting population has been considered in relation to mosquito activity in houses. It is possible, though, that some of those resting outside might have fed outside, without ever having entered houses at all. In an ordinary African village there is much human activity in the first hour or two after dark. At Tengeni, for instance, the children often ate their evening meal outside and there was much coming and going up to 21.00 hours, or sometimes later.

Accordingly, a small series of observations was made in order to gain an impression of the intensity of anopheline attack out of doors under conditions which bore some relation to normal happenings in the village.

Two men sat on chairs in a sheltered spot outside an experimental hut from 18.30 to 20.30 hours, while inside the hut more men were stationed. The two groups were changed over half way through the period. The outside group were usually supplemented by one or two small boys from the village, so that the outside bait was usually somewhat larger. Mosquitos were caught in test tubes as they settled to bite, torches being used to observe them.

TABLE VIII.

Outside biting (10 evenings).

	Indoors			Outdoors		
Time	*gambiae*	*funestus*	Other *Anopheles*	*gambiae*	*funestus*	Other *Anopheles*
18.30–20.30	9	9	5	10	2	25
20.30–05.00	272	327	—	—	—	—

The results of ten evening catches are set out in Table VIII, together with the numbers caught next morning in the experimental hut in which, from 20.30 hours onwards, two men slept.

Other workers have shown that there is very little biting activity at this period of the evening and, as might be expected, the numbers caught in the open, at a time when the people are outside, are of negligible importance in relation to the all-night house catches. Of the ten *gambiae* biting outside, eight were caught on one very still evening.

It seems likely, therefore, that the individuals of *gambiae* and *funestus* biting outside normally contribute little to the composition of the outside resting population.

The other *Anopheles* caught were *marshalli*, *coustani* (*tenebrosus* Dön. and type form), ~~*theileri*~~ *seydeli* Edw. and *leesoni*, in that order of frequency.

Discussion.

These investigations have shown that in the low-lying coastal belt of East Africa outside resting is a regular feature in the life history of both vector Anophelines. From the ratio of fed to gravid females in outside catches it is evident that little movement out of houses takes place during the first 12–24 hours after feeding. This is even more apparent if catches made near houses are disregarded, as being of doubtful validity. But during the later stages of the, in *gambiae* two-day and in *funestus* two- or three-day, gonotrophic cycle, free use of outside harbourages is made by both species.

The experience gained in this work has demonstrated again the extraordinary difficulties encountered in locating the natural outside resting sites of these African Anophelines. It is partly true that the shelters they choose are particularly secluded, but what is even more important is the likelihood that the total size of the adult population is relatively low when compared to that of vectors like *A. quadrimaculatus* in North America or *aquasalis* in Trinidad (Senior White, 1951). However big the fraction may be that rests outside, under African conditions the density of adults per unit of area must always be low and they will always be difficult to find, irrespective of the availability of suitable sites to the mosquito or their accessibility to the searcher. This may account for the failure of Wiseman and others (1939) to find *gambiae* outside in the Mombasa area.

Reference may be made to the conclusion of Hocking and MacInnes (1948), based on spray catches made daily in houses, that females of both species only rest outside immediately before or after egg-laying. Closer examination of these authors' figures suggests that their conclusions, as stated in this way, are misleading.

They recorded that the mean temperature at the time of the investigation was 25·5°C. (77·9°F.), which, as referred to above, is well above the critical temperature for a 48-hour cycle in *gambiae* and almost exactly the lower limit for a 48-hour cycle in *funestus*. Under these conditions, on the second day of the gonotrophic cycle the females are gravid and ready to lay the following night. They are therefore the "immediately before laying" group of Hocking and MacInnes, about the movements of which no evidence could be adduced from the methods they used. This work showed that on the first day after feeding, females tended to remain in houses, but it gave no information about the other, gravid, half of the population.

For this reason it cannot be agreed that evidence of exclusive house resting was produced by these authors, and their findings are, in fact, in accord with the observations recorded in this paper.

The observations on *gambiae* are in close agreement with earlier work from the coastal areas of East and West Africa by Muirhead Thomson, who has contributed a great deal to our knowledge of the behaviour of African

Anophelines, and focussed attention, in particular, on the partial use of outside resting places by this species. It has been possible to confirm and extend his work. Whether these same conclusions apply to higher and drier parts of the continent remains to be seen. Leeson's observations in Southern Rhodesia, that *gambiae* caught in houses were frequently fed and those caught outside were mainly gravid, certainly suggest that its behaviour there may not differ greatly from these findings at low altitudes.

In this context mention may be made of the doubtful value of the term "exophily" when applied without qualification to populations of this species found outside houses. It is obvious that *per se* the finding of gravid *gambiae* resting outside is not evidence for the existence of an exophilic race within the species. Such a conclusion must be based on the demonstration of an exodus of females from houses after feeding or the finding of fed specimens resting outside. In the studies reported here the numbers of fed females actually resting outside or caught leaving houses (as recorded in the second paper in this series (Gillies, 1954)), were far too small for any investigation of the possibility that this small fraction represented a distinct "exophilic" group or whether it was due to chance variation in the behaviour of individuals affecting the population as a whole. It appears that this group is of negligible importance in the East African area studied. This impression of the uniformity in behaviour of *gambiae* is strengthened by the failure of precipitin tests to reveal hosts other than man for females caught resting outside.

The actual proportion of the female population that rests outside at any particular stage of the gonotrophic cycle can only be determined by studying the composition of the house resting population. This subject will be considered in the second paper in this series (Gillies, 1954).

Summary.

The behaviour of *Anopheles gambiae* Giles and *A. funestus* Giles was studied under natural conditions in a lowland area of Tanganyika.

Studies on the outside resting population were carried out by direct searching for natural resting sites, and by the use of artificial box shelters partly buried in the ground in shaded localities. Catches in these give a valid sample when set up at some distance from houses.

Fed and gravid females comprised 67 per cent. of the outside resting *gambiae* population, the latter group being between 12 and 4·5 times as numerous as the former. Rather less than half the *funestus* females caught were unfed, the remainder of the population being mainly composed of gravid females.

Precipitin tests on the small numbers of fed females caught outside were nearly all positive for man.

The identification of gravid *funestus* females was confirmed by periodic examination of the eggs.

Entry of females into outside shelters did not occur solely in the period around sunrise. An appreciable number of *funestus* females did not enter before 07.00 hours and this was particularly so in shaded shelters.

The building of a hut in the vicinity of a box shelter caused a drastic reduction in the numbers of mosquitos resting in the latter.

Outside biting activity in these two species is of negligible importance as a source of females resting outside.

In this part of Africa, outside resting is deemed to be a regular occurrence in both these species during the second or third day of the gonotrophic cycle.

Acknowledgements.

My thanks are due to Dr. D. Bagster Wilson, Director of the East African Malaria Unit, for his helpful interest in this work and for advice in preparing this paper. I am also indebted to the many other members of the staff, whose assistance was essential to the completion of these investigations.

All the precipitin tests were carried out by Mr. B. Weitz, of the Lister Institute of Preventive Medicine, with the financial help of the Colonial Medical Research Committee, and grateful acknowledgement is made to him.

This work was carried out under the administration of the E.A. High Commission with funds provided by the East African Governments and by the Colonial Office from the research allocation of the Colonial Development and Welfare Acts on the recommendation of the Colonial Medical Research Committee.

References.

Blin, G. (1908). Déstruction des moustiques par le procédé des trous-pièges.—Bull. Soc. Path. exot., **1,** pp. 100–103.

De Meillon, B. (1934*a*). Observations on *Anopheles funestus* and *Anopheles gambiae* in the Transvaal.—Publ. S. Afr. Inst. med. Res., **6,** no. 32 pp. 195–248.

De Meillon, B. (1934*b*). Studies on insects of medical importance in South Africa.—Publ. S. Afr. Inst. med. Res., **6,** no. 33 pp. 249–307.

De Meillon, B. (1936). *Anopheles funestus* Giles and *Anopheles leesoni* Evans in human habitations and outdoor haunts.—Ann. trop. Med. Parasit., **30,** pp. 1–2.

De Meillon, B. (1947). The Anophelini of the Ethiopian geographical region.—Publ. S. Afr. Inst. med. Res., **10,** no. 49, 272 pp.

De Zulueta, J. (1950). A study of the habits of the adult mosquitoes dwelling in the Savannas of eastern Colombia.—Amer. J. trop. Med., **30,** pp. 325–339.

De Zulueta, J. (1952). Observations on mosquito density in an endemic malarious area in eastern Colombia.—Amer. J. trop. Med. Hyg., **1,** pp. 314–329.

Evans, A. M. & Garnham, P. C. C. (1936). The *funestus* series of *Anopheles* at Kisumu and a coastal locality in Kenya.—Ann. trop. Med. Parasit., **30,** pp. 511–520.

Evans, A. M. & Leeson, H. S. (1935). The *funestus* series of *Anopheles* in Southern Rhodesia, with description of a new variety.—Ann. trop. Med. Parasit., **29,** pp. 33–47.

Eyles, D. E. & Bishop, L. K. (1943). The microclimate of diurnal resting places of *Anopheles quadrimaculatus* Say in the vicinity of Reelfoot Lake.—Publ. Hlth Rep., **58,** pp. 217–230.

Gillies, M. T. (1953). The duration of the gonotrophic cycle in *Anopheles gambiae* and *Anopheles funestus*, with a note on the efficiency of hand catching.—E. Afr. med. J., **30,** pp. 129–135.

Gillies, M. T. (1954). Studies in house leaving and outside resting of *Anopheles gambiae* Giles and *Anopheles funestus* Giles in East Africa. II. The exodus from houses and house resting population.—Bull. ent. Res., **45,** pp. 375–387.

Hocking, K. S. & MacInnes, D. G. (1948). Notes on the bionomics of *Anopheles gambiae* and *Anopheles funestus* in East Africa.—Bull. ent. Res., **39,** pp. 453–465.

HOLSTEIN, M. H. (1952). Biologie d'*Anopheles gambiae*.—Monogr. Ser. World Hlth Org., no. 9, 176 pp.

LEESON, H. S. (1931). Anopheline mosquitoes in Southern Rhodesia, 1926–1928.—Mem. Lond. Sch. Hyg. trop. Med., no. 4, 55 pp.

MACAN, T. T. (1950). The anopheline mosquitoes of Iraq and north Persia.—Mem. Lond. Sch. Hyg. trop. Med., no. 7, pp. 109–219.

MUIRHEAD THOMSON, R. C. (1948). Studies on *Anopheles gambiae* and *A. melas* in and around Lagos.—Bull. ent. Res., **38**, pp. 527–558.

MUIRHEAD THOMSON, R. C. (1951*a*). Mosquito behaviour in relation to malaria transmission and control in the Tropics.—219 pp. London, Arnold.

MUIRHEAD THOMSON, R. C. (1951*b*). Studies on salt-water and fresh-water *Anopheles gambiae* on the East African coast. Bull. ent. Res., **41**, pp. 487–502.

RUSSELL, P. F. & SANTIAGO, D. (1934). An earth-lined trap for anopheline mosquitoes.—Proc. ent. Soc. Wash., **36**, pp. 1–21.

SENIOR WHITE, R. A. (1951). Studies on the bionomics of *Anopheles aquasalis* Curry, 1932. Part II.—Indian J. Malar., **5**, pp. 465–512.

SYMES, C. B. (1941). Malaria in Nairobi.—E. Afr. med. J., **17**, pp. 414–430.

WHARTON, R. H. (1950). Daytime resting places of *Anopheles maculatus* and other Anophelines in Malaya, with results of precipitin tests.—Med. J. Malaya, **4**, pp. 260–271.

WILSON, D. B. (1936). Report of the Malaria Unit, Tanga, 1933–34.—71 pp. Dar es Salaam, Govt. Printer.

WISEMAN, R. H., SYMES, C. B., MCMAHON, J. C. & TEESDALE, C. (1939). Report on a malaria survey of Mombasa.—60 pp. Nairobi, Govt. Printer.

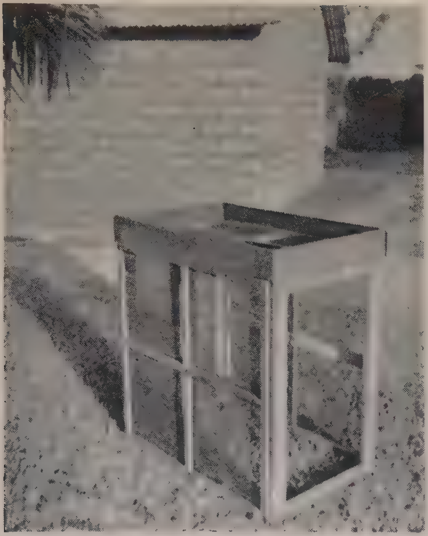


FIG. 1. Frame for box shelter.

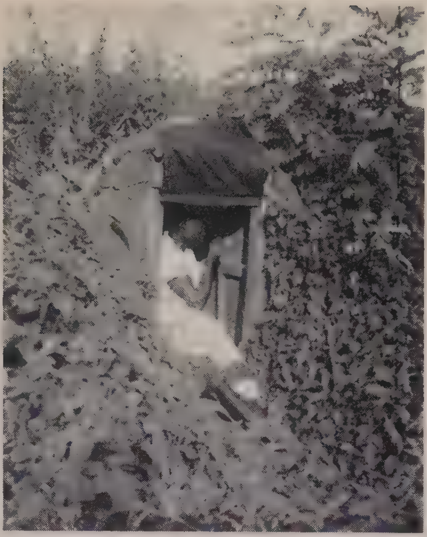


FIG. 2. Box shelter with curtain raised for catching mosquitos.

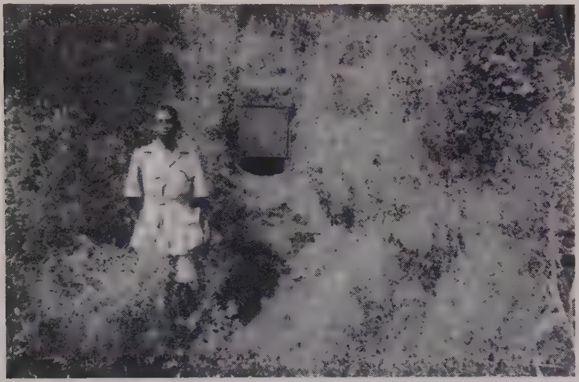


FIG. 3. Box shelter buried in earth bank with curtain lowered.

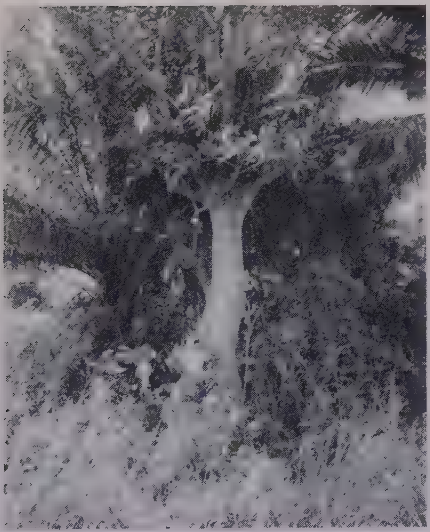


FIG. 4. Heavily shaded tree base, natural harbourage of *A. funestus*.

FIG. 5. Detail of the same tree base.

STUDIES IN HOUSE LEAVING AND OUTSIDE RESTING OF *ANOPHELES GAMBIAE* GILES AND *ANOPHELES FUNESTUS* GILES IN EAST AFRICA.

II.—THE EXODUS FROM HOUSES AND THE HOUSE RESTING POPULATION.

By M. T. Gillies.
East African Malaria Unit, Amani, Tanganyika.

Further observations on the composition and distribution of the daytime resting populations of *Anopheles gambiae* Giles and *Anopheles funestus* Giles are recorded in this paper. The studies reported here, which were carried out in a low-lying area of Tanganyika, are concerned with the exodus from houses of females at different stages of the gonotrophic cycle and with the composition of the house resting population. They must be regarded as complementary to those already described on the outside resting population (Gillies, 1954).

The predominantly house resting habits of *gambiae* and *funestus* have been known since the earliest observations on these insects (Ross, Annett & Austen, 1900). De Meillon (1947) has summarised the state of knowledge on this subject. Relatively little work however has been recorded on the composition of the house population in relation to their feeding and egg-laying activities. In West Africa, Muirhead Thomson (1951*a*) recorded that recently fed females of *gambiae* were 1·5 times as numerous in houses as gravid females. No such observations appear to have been published on *funestus* except for a small number of catches recorded by Hocking and MacInnes (1948). Most other observations have been of daily catches in experimental huts (Haddow, 1942; Ribbands, 1946), and such catches cannot of course be representative of the normal house resting population.

Before considering the mosquitos that may be caught in houses in the daytime, it may be convenient to describe experiments to determine the proportion that leave at different intervals after feeding. Those that feed in houses at night and leave before dawn will not appear in morning catches and, from the standpoint of control with residual insecticides, they are perhaps the most important group.

The Exodus after Feeding.

In these experiments two specially designed mud huts with thatched roofs were used, as described by Gillies (1953). The description is repeated here. These huts were solidly built with a cement floor, and the space between the top of the walls and eaves was carefully blocked in with mud. Five windows were incorporated with close-fitting shutters, which could be removed when more light was required inside the hut, or replaced by window traps. Entry for mosquitos was provided for by a line of slit shutters, 2½ inches high, on all sides of the hut just below the eaves. These could be operated from inside the hut and, when closed, the hut was effectively sealed. In order to facilitate the capture of mosquitos, a low ceiling of white cotton sheeting was installed in one of them, fitting flush with the walls just above the slit shutters. A single window trap was used in this hut. The other hut had three windows with traps, and a natural thatch roof with only the upper part sealed off with cotton sheeting. Hand-catching was employed throughout and, as previously shown (Gillies, 1953) it is believed that something like 85 per cent. of the daily resting population was caught. Two men slept in each hut.

The entry shutters were closed in the first hut every morning at 05.00–05.30 hours, 15–30 minutes before dawn. An alarm clock was provided to wake the sleepers. The other hut, in which the shutters were open continuously, was only used for 20 catches. In the first hut therefore mosquitos could escape at dawn only into the window traps.

There remained the possibility that some were flying out through the entry shutters during the night. To demonstrate this, one out of the eight shutters was fitted with a mosquito netting trap, which was left in place all night. The shutter chosen was altered once in the middle of the investigation in order to reduce position effects. As it was found that females were, in fact, escaping through the shutters during the night, a further short experiment was carried out in which four out of the eight entry shutters were fitted with traps.

In Table I the catches from these huts before and after the installation of first one, and then four, shutter traps are set out separately. All mosquitos referred to are blood-fed females.

TABLE I.

Exodus of blood-fed females.

				Numbers caught			Estimated exodus	
Species	Shutters with traps	No. of windows	No. of catches	Total catch (A)	Window traps (B)	Shutter traps	Nos. leaving through 8 shutters (C)	Total (B+C) as % of (A)
A. gambiae	0	3	20	144	0	—		
	0	1	13	253	1	—		
	1	1	174	1,826	11	13	104	6·3
	4	2	10	271	7	6	12	7·01
A. funestus	0	3	20	620	1	—		
	0	1	13	759	1	—		
	1	1	174	3,942	11	19	152	4·13
	4	2	10	166	1	7	14	9

In order to obtain the estimated exodus through all 8 shutters, the catches in shutter traps were multiplied by 8, where only one shutter was fitted with a trap, or by 2, where there were 4 with traps. The total leaving is this figure plus the window trap catches, expressed as a percentage of the total catch.

In these experiments less than one per cent. of either species attempted to leave after feeding and were caught in window traps. Similar negligible numbers were caught in the shutter traps; but in one experiment (174 catches) there were seven other shutters without traps, while in the other series (ten catches) half of the shutters, that is, four of them, were left open. It is possible therefore that eight times as many may have been leaving the huts during the course of the night in the first experiment, and twice as many in the second. This would give an estimated total leaving of 6·3 and 7 per cent. for *gambiae* in the two experiments, and 4·1 and 9 per cent. for *funestus*.

These results indicate that the exodus from houses after feeding is of the order of 4–8 per cent. in both species (the 9 per cent. calculated for *funestus* in the second experiment was based on rather small numbers). This suggests that only a very small number of females of *gambiae* or *funestus* will be missed in morning spray catches. As all the shutters were closed before dawn, it is evident that most of these individuals did not wait till then before leaving. There was, further, no greater tendency to leave the hut with three windows than that with only one. This latter hut, with its low white cotton ceiling, was a great deal lighter than any ordinary African house, yet no appreciable exodus was detected.

A further point should be noted. Of 30 *gambiae* caught leaving after feeding, one half were found to be newly emerged females, as will be shown in a later paper. Thus the actual percentage of females leaving after later blood meals will be even smaller than the figure given above. Similar observations were also made on *funestus*.

These findings agree closely with those of Muirhead Thomson (1951*b*) in Dar-es-Salaam, who found that not more than 2 per cent. of fresh-water *gambiae* and of *funestus* left after feeding. From West Africa there are reports of a much greater exodus of fed *gambiae* from houses, and it has been suggested that this can be correlated with the type of breeding site from which the females originated (Holstein, 1949; Campbell, 1951). The catches recorded here were carried out over a period of eight months, from April to December, without any alteration in the behaviour of *gambiae* being detected. This period of observation included two short rainy seasons and several months of dry season, when *gambiae* breeding sites might be assumed to be mainly " temporary " and " permanent " respectively. If any striking difference in the affinity for house resting of *gambiae* originating from different breeding sites were to occur in this area, one would have expected some seasonal change to be apparent in experiments of this nature.

Only occasional specimens of other Anophelines were caught in these huts. A single specimen of *A. squamosus* Theo., for instance, was caught in a window trap, although no other specimens were found in numerous spray catches in houses in the area. Small numbers of *Taeniorhynchus* (*Mansonioides*) *africanus* (Theo.) and *T.* (*M.*) *uniformis* (Theo.) were caught, and 64 of 150 specimens were found in window traps. On the other hand, only 4 out of 913 *Culex pipiens fatigans* Wied. were found in the traps.

Exodus of Half-Gravid Females.

The exodus of females from houses 24 hours after entering, when the ovaries are still only partly developed, was also studied.

The views expressed by other workers on the duration of the stay of females in houses have been rather conflicting. While some of these differences may be geographical, or dependent on climatic conditions or on the type of house observed, some of them appear to be due to the methods employed and the deductions drawn from them. Thus Gordon and others (1932) used mosquitos that were caught, marked with stain and then released in houses. Less than 5 per cent. of marked females were recovered in the houses 24 hours later. Causey, Deane and Deane (1943) obtained similar results with *gambiae* in Brazil.

Hocking and MacInnes (1948), approaching the problem indirectly, carried out daily spraying and found no diminution in the numbers caught on subsequent days. They concluded that there was a 100 per cent. daily turnover of both *gambiae* and *funestus*. Muirhead Thomson (1948, 1951*b*) in both East and West Africa made direct observations, by the use of window traps, on the numbers leaving houses. He found that about 33 per cent. left when half-gravid, although not ready to oviposit for another 24 hours. Marking methods are open to the objection that gross handling of the mosquitos is involved and their subsequent behaviour cannot be taken as natural. It is considered that the direct approach with window traps is more likely to give a reliable picture of normal behaviour, though the use of experimental huts will probably give results on the low side, owing to the lack of disturbance from occupants.

A small series of observations on these lines was accordingly carried out.

In the experimental hut described, catches were made on five days a week over a period of ten weeks. On the fifth morning of each week, instead of making the usual morning catch, the house was locked up, and two window traps put in position on the west side of the hut. It was re-visited 45 to 60 minutes after nightfall, the traps were removed, and two other traps put back in their place. The hut then remained locked up and empty, and with all shutters closed throughout the night. Next morning the window traps were inspected, and a normal hand-catch of all mosquitos resting in the hut made as usual. In this way it was possible to catch those leaving at dusk, those leaving during the night and the following dawn, and those remaining in the hut for the full 48 hours.

The following results were obtained in ten catches made during the hot season. Only those females are recorded in which maturation of the ovaries followed the blood meal, *i.e.*, true half-gravid females. No *gambiae* and only two *funestus* attempted to leave during the night and these have been counted in with the evening exodus.

TABLE II.

The evening exodus of half-gravid females (10 catches).

	A. gambiae			*A. funestus*		
	Leaving	Remaining	Total	Leaving	Remaining	Total
Numbers	61	81	142	12	373	385
Per cent.	43	57		3·1	96·8	

This aspect of the behaviour of *gambiae* has already been demonstrated by Muirhead Thomson in Dar-es-Salaam and his figures agree closely with the findings in Table II. While the numbers of *gambiae* in this series are small, the difference in behaviour between this species and *funestus* is very striking.

The numbers of half-gravid *gambiae* leaving the experimental hut at dusk constituted 43 per cent. of those that had entered 12–24 hours earlier for a blood meal. Only 3 per cent. of *funestus* left under the same conditions. This suggests a greater tendency of *gambiae* to leave the shelter of houses and to make use of outside resting places during the second half of the gonotrophic cycle.

The Daytime House Resting Population.

Spray catches in houses.

The mosquito population of houses is best studied by spray-catching with pyrethrum. Care should be taken that sufficient houses in the area are sprayed, in order to even out differences in the numbers of occupants and in the construction of the houses. The catches should also be made at frequent intervals in order to avoid the effects of day to day fluctuations in the biting population of mosquitos. No house should be re-sprayed more than once in a week, and adequate cotton sheeting should be used to cover the whole floor space of all rooms in a hut.

The results of 176 spray-catches in the village of Tengeni are set out in Tables III and IV. Catches made in the hot and the cool season are presented separately. The hot season comprises those months of the year, mid-November to the first half of May, when the mean monthly temperature exceeds 78°F. The cool season catches were made from June to August when the mean temperature varied from 73°F. to 75°F. with occasional cooler days. The catches are classified as Unfed, Fed and Gravid, as already defined in Part I of this series (Gillies, 1954).

TABLE III.

Spray catches from African houses.

Season	No. of catches	Unfed		Fed		Gravid		Total
		Nos.	%	Nos.	%	Nos.	%	
				A. gambiae				
Hot ..	140	480	4·3	7,158	65	3,382	30·7	11,020
Cool ..	36	28	3·6	438	56·5	309	39·9	775
				A. funestus				
Hot ..	133	1,551	13·7	5,746	50·9	3,994	35·4	11,291
Cool ..	36	263	5·9	2,004	45·4	2,151	48·7	4,418

TABLE IV.

Composition of house catches; ratios of fed: gravid females.

Season	*A. gambiae*		*A. funestus*	
	Fed	Gravid	Fed	Gravid
Hot ..	1	0·47	1	0·7
Cool ..	1	0·7	1	1·07

It is known that the gonotrophic cycle in both species lasts two days at temperatures above 78°F., and in *funestus* for three days at temperatures below 76·5°F. (Gillies, 1953). It is clear from Table IV therefore that a proportion of gravid females, those in the second or third day of the cycle, are absent from houses, and this is strongly suggestive of the use of outside resting sites. It is also evident that the parity of fed and gravid *funestus* females in the cool season is the outcome of a longer cycle and not of a reduced exodus of gravid females. Similarly the contrast in the numbers of *gambiae* and *funestus* in houses must be due to a greater use of outside resting sites by the former species.

Mosquito population of open or unoccupied houses.

The figures in Table V illustrate the influence of the construction of a particular house on the composition of the daytime resting population. The "open" house was one in which there was wide separation between the roof and the top of the walls, and between the four sections of the roof. As a result of this it was very much lighter and more open than the average hut, light enough in fact for one to be able to see to read in the bedroom. The catches were made in the hot season.

In the open house it is seen that there was a great excess of gravid over fed *funestus* females. As the gonotrophic cycle lasted only 48 hours at this time of year, this excess must have been due to re-entry, probably at dawn, of females that had left other houses. The catches of *gambiae* show no such distinction between the two types of house, which suggests that dawn re-entry of gravid females occurs to a much lesser extent. These figures show that, while the exodus at dusk of half-gravid females may or may not be affected by the degree of openness of the houses, this may be more than counteracted in the case of *funestus* by those re-entering at dawn.

TABLE V.

Spray catches from an "open" house.

Species	Unfed		Fed		Gravid		Total
	Nos.	%	Nos.	%	Nos.	%	
A. gambiae ..	38	4·7	484	59·8	287	35·5	809
A. funestus ..	72	7	391	37·8	569	55·2	1,032

Contrary to previous impressions relating mainly to *gambiae* (Gordon & others, 1932; Causey, Deane and Deane, 1943), this particular type of house is shown to have a larger net daytime resting population of *funestus* than the ordinary house. It is probable that, in the case of re-entry at dawn, the degree of lightness inside the house is of secondary importance compared with the number of openings available to females seeking shelter.

Further evidence in support of this suggestion comes from hand-catches made on the outskirts of the village in an unoccupied hut that was in a state of considerable disrepair. This house harboured large numbers of males and both unfed and gravid females, as shown in Table VI.

TABLE VI.

Catches from an empty house.

Species	Unfed	Fed	Gravid	Total
A. gambiae ..	28	7	140	175
A. funestus ..	138	11	441	590

It is clear that the population is composed mostly of females that have left houses in the later stages of the gonotrophic cycle. Had this empty house not been available, these females might have flown on at dawn and re-entered occupied houses or else remained in outside resting sites. It seems logical to suggest that the proportion, in the case of *funestus* at least, of unfed and gravid females resting outside, may be determined by the number of houses in relation to the number and proximity of suitable outside shelters.

Catches of gravid *gambiae* and *funestus* females, made in African houses in the daytime during the hot season, are respectively 53 per cent. and 30 per cent. lower than the corresponding numbers of recently fed specimens. Their absence is attributed to the partial use of outside resting sites by these females.

A particularly open type of house was found to harbour an excess of gravid *funestus* females. This is indicative of the extent to which re-entry at dawn may take place.

Mortality During House Resting.

Consideration of the infection rates and probable longevity of both *gambiae* and *funestus* (Macdonald, 1952) leads one to expect that the mortality between feeding and the maturation of the eggs will be low, and will be mainly suffered in seeking blood meals and laying eggs. The intervals spent resting in houses should be attended by a relatively slight mortality, the result of infrequent contact with wall lizards or jumping spiders and predatory insects. The following evidence is brought forward in support of this suggestion.

In the observations already described on the exodus of half-gravid females at dusk it was explained that daily catches in an experimental hut were made on four mornings a week, and that on the fifth morning the hut was locked up empty, the window traps changed and no catch of mosquitos made until the sixth morning. It was also shown that a negligible number of half-gravid *funestus* (3 per cent.) attempted to leave and were caught in the window traps on the fifth evening. The catch of gravid females made on the following morning was therefore exactly comparable to the catches of fed females made on ordinary days and kept in the hut until being sorted the next day and the gravid females then counted. The only difference lay in that in one case they were resting on the walls and ceilings for 24 hours, and in the other they were inside a small cage protected from ants and spiders. Any gross mortality suffered by the *funestus* population during this 24 hours should become evident by comparing the average normal catch for the week with the delayed catch made on one day of the week.

The results of catches made over eight such weeks are shown in Table VII.

The average delayed catch differs from the average normal catch by only 4·1 mosquitos, nearly all the disparity being accounted for by the single low catch on May 9th. The value of t for the difference between the two means is 1·203 ($P = 0{\cdot}05$, $t = 2{\cdot}365$), and thus these figures do not show any significant difference between the two types of catch.

TABLE VII.

Mortality during house resting; catches of gravid *A. funestus* in experimental hut.

Period	Normal catches	Number of normal nights	Weekly normal average	Weekly delayed catch
21–25 Apr. ..	181	4	45·25	48
28 Apr.–2 May ..	261	3	87	79
5–9 May ..	133	2	66·5	35
12–16 May ..	163	4	40·75	43
19–23 May ..	80	3	26·7	27
26–30 May ..	132	4	33	27
2–6 June ..	186	4	46·5	36
9–13 June ..	149	4	37·25	39
Totals	1,285	28		334
Averages ..			45·9	41·75

Although no mortality could be detected amongst *funestus* females resting for 24 hours inside a house, it must be pointed out that these observations were carried out in an experimental hut which, while appearing to harbour an appreciable population of spiders and other insects, was unnatural in one important particular, in that the roof was screened off by a low cotton ceiling. The findings cannot therefore be applied, without further investigation, to normal African huts with roofs of thatch inhabited by a variety of predacious creatures.

Analysis of Unfed Females.

It is generally assumed that most tropical Anophelines require a single blood meal for the production of a single egg batch. Observations, which are being continued, made during the course of these investigations have confirmed the general but not invariable truth of this statement. On this assumption, and the knowledge ascertained on the duration of the gonotrophic cycle, it is desirable to find out the proportion of females returning to bite, after laying eggs, during the course of the same night.

In West Africa, Muirhead Thomson (1948) reported that experiments with marked *gambiae* indicated their return to houses to bite again without delay after oviposition. But he gave no figures, and the nature of the method is unlikely to show the proportion of females that succeed in so doing. However, study of the ovarian stages of all mosquitos caught by day in houses and in outside resting sites provides useful information on this question.

The ovaries of unfed females that have laid eggs are at Christophers' Stage II, and can be readily distinguished from unfed virgin females with Stage I ovaries. These unfed, multiparous females, that are found in daytime catches, may conveniently be described as "post-gravid." If one ignores the mortality involved in the search for a suitable breeding site and in the act of oviposition, then daytime catches will show equal numbers of females ready to lay eggs the next night, and of females that have already laid the night before. The former group will all be gravid, but the latter will be recognisable only if they are post-gravid and have not fed. If none have fed, the ratio of post-gravid to gravid females in the overall population will be 1 : 1. Any tendency of females to feed again after oviposition will result in their removal from the post-gravid group, which is by definition unfed, and the ratio will be correspondingly reduced.

The following Table sets out the numbers of virgin, post-gravid and gravid females from all the catches in houses and outside shelters, in which dissections of unfed females were made, and the corresponding ratios.

TABLE VIII.

Unfed and gravid females in daytime catches.

	A. gambiae			*A. funestus*		
	Unfed		Gravid	Unfed		Gravid
	Virgin	Post-gravid		Virgin	Post-gravid	
Ovarian Stage ..	I	II	V	I	II	V
In houses, nos. ..	18	25	358	176	129	1,032
do., ratio		1	14·3		1	8
Outside, nos. ..	168	18	292	398	119	545
do., ratio		1	16·2		1	4·6

A printer's error occurred in the final printing off of volume 45, part 2, page 383. Line 28, " females . . . density of " should be replaced by

" females available for daytime biting activities should environmental conditions "

It has already been shown that about 50 per cent. of *gambiae* have left the shelter of houses by the second day after a blood meal. Applying this distribution of the daytime resting gravid population to the above ratios, $\frac{14\cdot3 + 16\cdot2}{2} = 15\cdot25$, it is seen that there are 15 times as many *gambiae* females in the whole population ready to oviposit as there are individuals that have laid eggs and failed to feed again the same night.

This figure is influenced by two other factors, the relative importance of which cannot be assessed for the moment. Firstly, it may be lowered by the unknown mortality suffered by females in the course of oviposition and, secondly, it may be raised by the inclusion in the post-gravid group of females with Stage II ovaries that have not yet laid eggs. Evidence has been accumulated to show that, in a proportion of the biting population that is predominantly composed of new emergences, ingestion of blood is not followed by maturation of the ovaries beyond Stage II. If these females fail to obtain a second blood meal before the first has been digested completely, they will be found to be unfed and with ovaries in Stage II.

The figures of post-gravid *funestus* females were obtained from catches made over the whole year, so that the complication introduced by the longer gonotrophic cycle in certain seasons, and the associated differences in the proportion of gravid females resting outside, makes it impossible to assess the overall density of post-gravid females. Nevertheless, the catches show that both in and out of houses there is a much higher proportion of post-gravid *funestus* than *gambiae*. This could be due to a lesser mortality during oviposition, but it seems likely that it demonstrates a tendency in this species to lay eggs later in the night, or a lesser determination to feed again immediately afterwards.

The density of post-gravid females, together with an unknown proportion of virgin females, in daytime catches is an indication of the numbers of unsatisfied females ×~~resting outside, makes it impossible to assess the overall density of~~ ×× permit. It is evident that in the *gambiae* population studied by Haddow, Gillett and Highton (1947) in uninhabited forest in Uganda, which bit readily by day, a large number of unsatisfied females must have been present. This departure from "normal" behaviour may be as much due to the absence of the preferred host, man, as to factors associated with a forest environment. In a populous district such as Tengeni, the relationship of mosquito to man is close enough to ensure that relatively few females fail to obtain another blood meal before being forced to find shelter for the day.

Few females of *funestus* and even fewer of *gambiae*, that have survived the hazards of oviposition, can be found unfed the following day. It follows that the majority of females bite every 48 hours when the gonotrophic cycle lasts two days, or every 72 hours when the cycle is lengthened under cooler conditions.

Discussion.

In Part I of this series (Gillies, 1954) it was shown that catches of both *gambiae* and *funestus*, made outside, were mainly composed of gravid and unfed females and that few fed females were found. It was suggested that these facts were compatible with a very reduced exodus of females immediately after feeding but with a more substantial movement into outside resting sites in the middle of the gonotrophic cycle. This interpretation is amply confirmed by the findings reported here.

It was found with both species that an exodus of the order of 5 per cent. occurred immediately after feeding (p. 377), and this is in full accordance with the results of catches made outside. Since this negligible exodus of fed females occurs, and the duration of the gonotrophic cycle is known, it is permissible to use the ratio of fed to gravid females in houses as a means of estimating the

× available for daytime biting activities should environmental conditions ××

proportion of gravid females resting outside. Thus in the hot season about 50 per cent. of gravid *gambiae* and 30 per cent. of gravid *funestus* must be resting outside (p. 380). For a short period in the cool season the cycle in an unknown proportion of the *gambiae* population may last three days, and use cannot be made of this method of estimation. But in *funestus* the cycle lasts three days in the great majority of females throughout this period, and under these conditions the ratio of fed to gravid, in the whole population, must increase from 1 : 1 to 1 : 2. Of 100 fed and gravid females in the hot season the house resting population must consist of 50 fed females and 35 gravid females (see Table IV). Of a similar 100 females in the cool season 34 will be fed and resting in houses (ignoring the 5 per cent. that may be resting outside), 33 will be half-gravid or gravid and resting in houses, and 33 will be half-gravid or gravid and resting outside. Thus the numbers in the later stages of ovarian development resting in houses will remain more or less constant throughout the year, while the outside resting population of half-gravid and gravid females will be doubled. Use of this phenomenon has already been made in assessing the validity of catches in artificial outside shelters, as described in Part I of this series.

Catches made in window traps at dusk, demonstrated that many *gambiae* leave an undisturbed hut 24 hours before they are ready to lay eggs, and thereby come to constitute the major element in the outside resting population. Similar

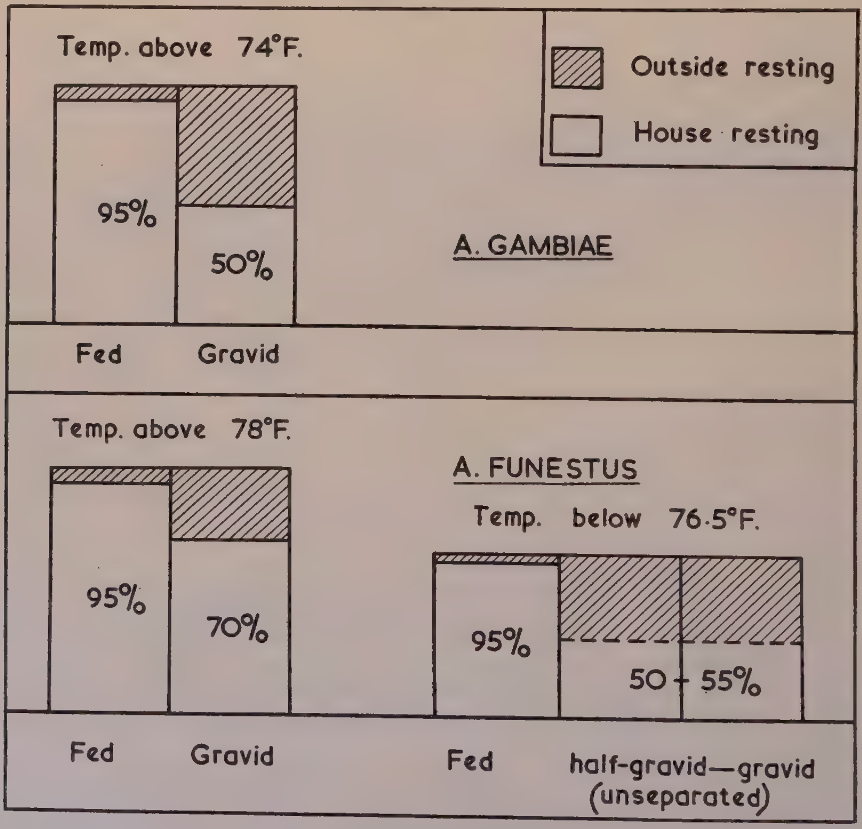


Fig. 1.—Diagrammatic representation of the distribution of the daytime resting population of *A. gambiae* and *A. funestus.*

catches of *funestus* suggested that very few females would leave at this stage, but the results of spray catches make it clear that, in normal houses with wide open doors and much bustle and activity, the exodus is of much greater proportions, though still less than *gambiae*. The results from an experimental hut are of interest for the indication they give of an inherent difference in behaviour between the two species, a distinction that is not so readily apparent from observations of their activity under strictly natural conditions.

From the above evidence it is possible to construct a composite picture of the distribution of the daytime resting populations of both *gambiae* and *funestus*. This is represented diagrammatically in fig. 1.

Spray catching in houses is commonly used to obtain a measure of the size of populations of African Anophelines. If the unfed section of females is ignored, consideration of this diagram shows that, where the gonotrophic cycle lasts two days, the house catches will represent some 70–75 per cent. of the *gambiae* and 80–85 per cent. of the *funestus* population. Under cooler conditions two-thirds of the *funestus* females will be caught in houses. In interpreting the results of such catches these facts should be borne in mind.

It is considered that the method of study, in which observations are made on both the house resting and the outside resting populations of a domestic Anopheline, and in which the source of the blood meal in both groups is determined, provides the surest basis for a balanced view of the behaviour of a species as a whole. In this investigation precipitin tests were not carried out on the house resting population, owing to the absence of cattle and the insignificant numbers of sheep and goats in the area. Other methods, such as catches on human or animal bait, can provide useful information about particular sections of a population. But they should always be combined with studies on females resting in as wide a variety as possible of daytime harbourages. Information derived from the former method could, under particular circumstances, also form the means whereby estimation of the total size of the population in an area could be made.

Summary.

Observations on the behaviour of *Anopheles gambiae* Giles and *A. funestus* Giles in experimental huts and ordinary African houses were carried out in a low-lying area of Tanganyika. Special attention was paid to the exodus of females at different stages of the gonotrophic cycle and to the composition in terms of ovarian development of the house resting population.

About 5 per cent. of the biting population of *gambiae* and the same number of *funestus* were shown by the use of window traps to be leaving experimental huts after feeding.

Forty three per cent. of half-gravid *gambiae* left an experimental hut at dusk, 12–24 hours after entering for a blood meal, whereas only 3 per cent. of *funestus* left under the same conditions.

Daytime spray catches of gravid *gambiae* and *funestus* made in ordinary African houses during the hot season were about 50 per cent. and 30 per cent. lower, respectively, than the corresponding numbers of recently fed specimens. *A. funestus* therefore makes rather less use of outside shelters than *gambiae* during the hot months.

In the cool season about 50 per cent. of half-gravid and gravid *funestus* were absent from house catches.

No mortality could be detected amongst *funestus* females resting under natural conditions for 24 hours in an experimental hut.

Re-entry of gravid *funestus* into unoccupied and open types of inhabited houses occurs at dawn.

Analysis of ovarian development in unfed females shows that the great majority

of *gambiae* and *funestus* feed every other night when the gonotrophic cycle lasts two days, and every three nights when the cycle lasts three days.

A composite picture of the distribution of the daytime resting populations derived from these results shows that, when the gonotrophic cycle lasts two days, about 5 per cent. of *gambiae* rest outside when blood-fed, and about 50 per cent. when gravid. About 5 per cent. of *funestus* rest outside when fed, and 30 per cent. when gravid. Under cooler conditions and a three-day cycle some 50 per cent. of *funestus* spend the second and third days of the cycle resting outside.

Acknowledgements.

Dr. D. Bagster Wilson, Director of the East African Malaria Unit, gave valuable advice in preparing this paper. Much of the work recorded in Parts I and II of this series was only made possible by the constant assistance of Mr. C. D. Ramsdale in collecting, dissecting and supervision. Mr. M. C. F. Butler also participated in many of the investigations. The help of both these two Field Officers is gratefully acknowledged. Mention should also be made of the many members of the African staff and students in training, who at different times were engaged in this work. In particular the help of the Malaria Assistants, A. J. Osumbah and F. J. Ojjiki was most valuable.

This work was carried out under the administration of the E. A. High Commission with funds provided by the East African Governments and by the Colonial Office from the research allocation of the Colonial Development and Welfare Acts on the recommendation of the Colonial Medical Research Committee.

References.

Campbell, R. W. H. (1951). A preliminary statistical study of *Anopheles gambiae* Giles, based on maxillary indices.—Bull. ent. Res., **42,** pp. 647–658.

Causey, O. R., Deane, L. M. & Deane, M. P. (1943). Ecology of *Anopheles gambiae* in Brazil.—Amer. J. trop. Med., **23,** pp. 73–94.

De Meillon, B. (1947). The Anophelini of the Ethiopian geographical region.—Publ. S. Afr. Inst. med. Res., **10,** no. 49, 272 pp.

Gillies, M. T. (1953). The duration of the gonotrophic cycle in *Anopheles gambiae* and *Anopheles funestus*, with a note on the efficiency of hand catching.—E. Afr. med. J., **30,** pp. 129–135.

Gillies, M. T. (1954). Studies in house leaving and outside resting of *Anopheles gambiae* Giles and *Anopheles funestus* Giles in East Africa. I. The outside resting population.—Bull. ent. Res., **45,** pp. 361–373.

Gordon, R. M., Hicks, E. P., Davey, T. H. & Watson, M. (1932). A study of the house-haunting Culicidae occurring in Freetown, Sierra Leone.—Ann. trop. Med. Parasit. **26,** pp. 273–345.

Haddow, A. J. (1942). The mosquito fauna and climate of native huts at Kisumu, Kenya.—Bull. ent. Res., **33,** pp. 91–142.

Haddow, A. J., Gillett, J. D. & Highton, R. B. (1947). The mosquitoes of Bwamba County, Uganda. Part V. The vertical distribution and biting-cycle of mosquitoes in rain-forest with further observations on microclimate.—Bull. ent. Res., **37,** pp. 301–330.

Hocking, K. S. & MacInnes, D. G. (1948). Notes on the bionomics of *Anopheles gambiae* and *Anopheles funestus* in East Africa.—Bull. ent. Res., **39,** pp. 453–465.

Holstein, M. H. (1949). Le problème d'*Anopheles gambiae*.—Bull. méd. A.O.F., **1949,** no. spéc., pp. 155–160.

MACDONALD, G. (1952). The analysis of the sporozoite rate.—Trop. Dis. Bull., **49**, pp. 569–586.

MUIRHEAD THOMSON, R. C. (1948). Studies on *Anopheles gambiae* and *A. melas* in and around Lagos.—Bull. ent. Res., **38**, pp. 527–558.

MUIRHEAD THOMSON, R. C. (1951*a*). Mosquito behaviour in relation to malaria transmission and control in the Tropics. 219 pp. London, Arnold.

MUIRHEAD THOMSON, R. C. (1951*b*). Studies on salt-water and fresh-water *Anopheles gambiae* on the East African coast.—Bull. ent. Res., **41**, pp. 487–502.

RIBBANDS, C. R. (1946). Moonlight and house-haunting habits of female Anophelines in West Africa.—Bull. ent. Res., **36**, pp. 395–417.

ROSS, R., ANNETT, H. E. & AUSTEN, E. E. (1900). Report of the Malaria Expedition of the Liverpool School of Tropical Medicine and Medical Parasitology.—Mem. Lpool Sch. trop. Med., no. 2, 58 pp.

THE SPECIES OF *CARPOPHILUS* STEPHENS (COL. NITIDULIDAE) ASSOCIATED WITH STORED PRODUCTS.

By Ronald M. Dobson. E.H.N.
*Wye College, University of London.**

The genus *Carpophilus* Stephens is almost cosmopolitan in distribution and over 180 species, mostly from tropical and subtropical regions, have been described. Sixteen species have been found in association with stored products in different parts of the world and several of these are continually distributed by international trade and have become established in many countries.

Of the twelve species which have been found in Britain, *Carpophilus hemipterus* (L.), *C. dimidiatus* (F.), *C. ligneus* Murr. and *C. obsoletus* Er. are frequently introduced on foodstuffs and are now established. They are serious pests of commodities such as dried fruit which pass to the consumer with little or no processing.

C. mutilatus Er. and *C. maculatus* Murr., though introduced less frequently, sometimes occur in considerable numbers. *C. flavipes* Murr., *C. marginellus* Mots., *C. humeralis* (F.), *C. nitidus* Murr. and *C. succisus* Er. have been imported occasionally in small numbers. The status of *C. fumatus* Boh. as a pest of stored products is uncertain. There is no definite record of its having occurred, but since it closely resembles *C. mutilatus* Er. it is included in this paper. According to Fowler (1889) the rare British species *C. sexpustulatus* (F.) has occurred in dried fruit.

C. pallipennis (Say), *C. niger* (Say), *C. immaculatus* Lucas and *C. nitidulus* Fletcher have all been recorded as having occurred on stored products, but not in Britain. Because it was not possible to examine specimens of the last two species neither has been included in this paper. The name *C. nitidulus* Fletcher could not be traced. *C. davidsoni* Dobson has been found in Australia infesting sweet corn, figs and peaches. It was not clear whether these were in storage or not, but the inclusion of this species here seems advisable.

The present account is intended to supplement the work of Hinton (1945) and several species which were not fully described by him or were only recently recorded in stored products are described. His key has been modified and extended to include these additions, and some characters of taxonomic value have been figured.

The lateral lobes of the aedeagus of each species in the key, except *C. nitidus* and *C. succisus*, and the internal 8th sternite of the male of each, except *C. mutilatus*, *C. nitidus* and *C. fumatus*, have been figured (figs. 10–23 and 24–36) as these parts differ considerably even between closely related species and provide a useful check on identity. Figs. 16, 17, 18 and 20 have been published previously (Dobson, 1952). The female genitalia are of little taxonomic value as they are very similar in related species. In *C. maculatus* and *C. mutilatus* (fig. 39) the female genitalia are very similar but differ considerably from those of *C. dimidiatus* (fig. 38) although they have frequently been regarded as synonymous with or varieties of the latter. The female genitalia of *C. obsoletus* are illustrated (fig. 37) as this species has frequently been confused with *C. dimidiatus*.

The drawings were made from preparations of specimens lent by the British

---

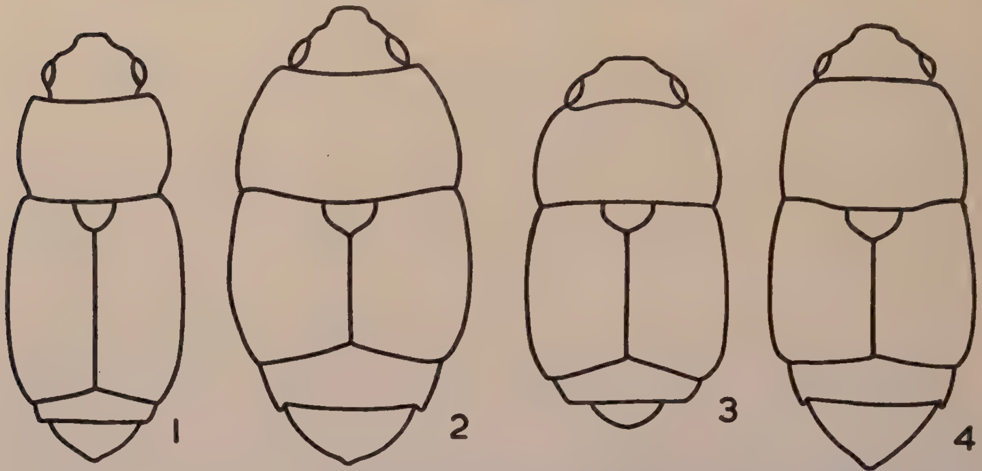
* Now at Rothamsted Experimental Station, Harpenden, Herts.

Museum (Nat. Hist.) and by Dr. H. E. Hinton, of the Department of Zoology at Bristol University.

Key to Species.

1 (2) Three abdominal tergites visible behind apex of elytra in both sexes. ... 3

2 (1) Two abdominal tergites visible behind apex of elytra in both sexes. (N.B.—In abnormally extended specimens three tergites may be visible, but if this is the case the most anterior of these is much shorter than the penultimate and is less heavily sclerotised.) 5



Figs. 1–4.—Body form of *Carpophilus* species: (1) *C. sexpustulatus*; (2) *C. flavipes*; (3) *C. succisus*; (4) *C. obsoletus*.

3 (4) Lateral margin of prothorax when viewed from side appearing of equal thickness from apex to base or only slightly thicker at apex than at base. .... *C. nitidus* Murr.

4 (3) Lateral margin of prothorax when viewed from side twice as thick at apex as at base, the increase in thickness occurring rather sharply midway between base and apex. .... *C. humeralis* (F.) (figs. 10 & 24)

5 (6) Length of elytral suture when measured from apex to scutellum almost twice as great as length of pronotum along midline (fig. 1). .... *C. sexpustulatus* (F.) (figs. 11 & 25)

6 (5) Elytral suture about equal in length to pronotum 7

7 (8) Line bordering caudal rim of mesocoxal cavity parallel to cavity along its median third, and then diverging postero-laterally so as to meet metepisternum at or posterior to the mid-point between its apex and base. The axillary area thus defined is very large (fig. 5). 9

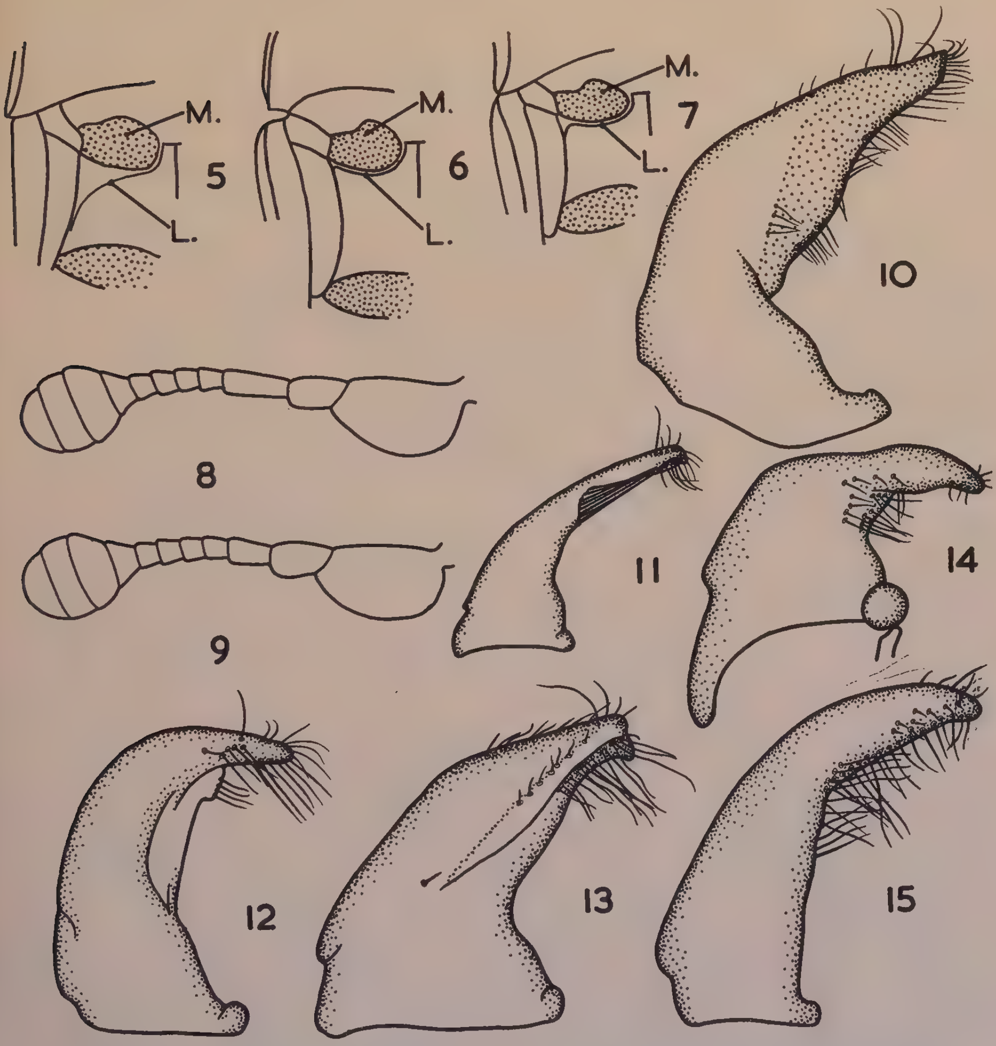
8 (7) Line bordering caudal rim of mesocoxal cavity parallel to cavity except at extreme sides or diverging from cavity about its lateral third so as to meet the metepisternum within its anterior third. The axillary area is here much smaller than it is in the above case. 11

9 (10) Mesosternum with a median longitudinal carina. Texture of surface within axillary area similar to that of remainder of metasternum at sides. .... *C. marginellus* Mots. (figs. 12 & 26)

10 (9) Mesosternum evenly convex and with no trace of a median longitudinal carina. Texture of surface within axillary area markedly different from that of remainder of metasternum at sides. Body shape as fig. 3. ...... *C. succisus* Er. (fig. 27)

11 (12) Line bordering caudal rim of mesocoxal cavity parallel to cavity except at extreme sides where it diverges slightly posteriorly so as to end opposite to, or just behind the anterior margin of the metepisternum (fig. 6). .... (13)

12 (11) Line bordering caudal rim of mesocoxal cavity diverging posteriorly from the cavity so that laterally it is at least three times as far from the cavity as it is near the midline, and usually meets the metepisternum at about its anterior fourth, or approaches the metepisternum as though to meet it and then diverges posteriorly once more and runs parallel to its margin or meets it in an asymptotic manner (fig. 7). .... (19)



Figs. 5–7.—Ventral aspect of mesothorax to show form of line bordering caudal rim of mesocoxal cavity: M—mesocoxal cavity; L—line. (5) *C. marginellus*; (6) *C. ligneus*; (7) *C. dimidiatus*.

Figs. 8–9.—Antennae of *Carpophilus* species. (8) *C. dimidiatus*; (9) *C. mutilatus*.

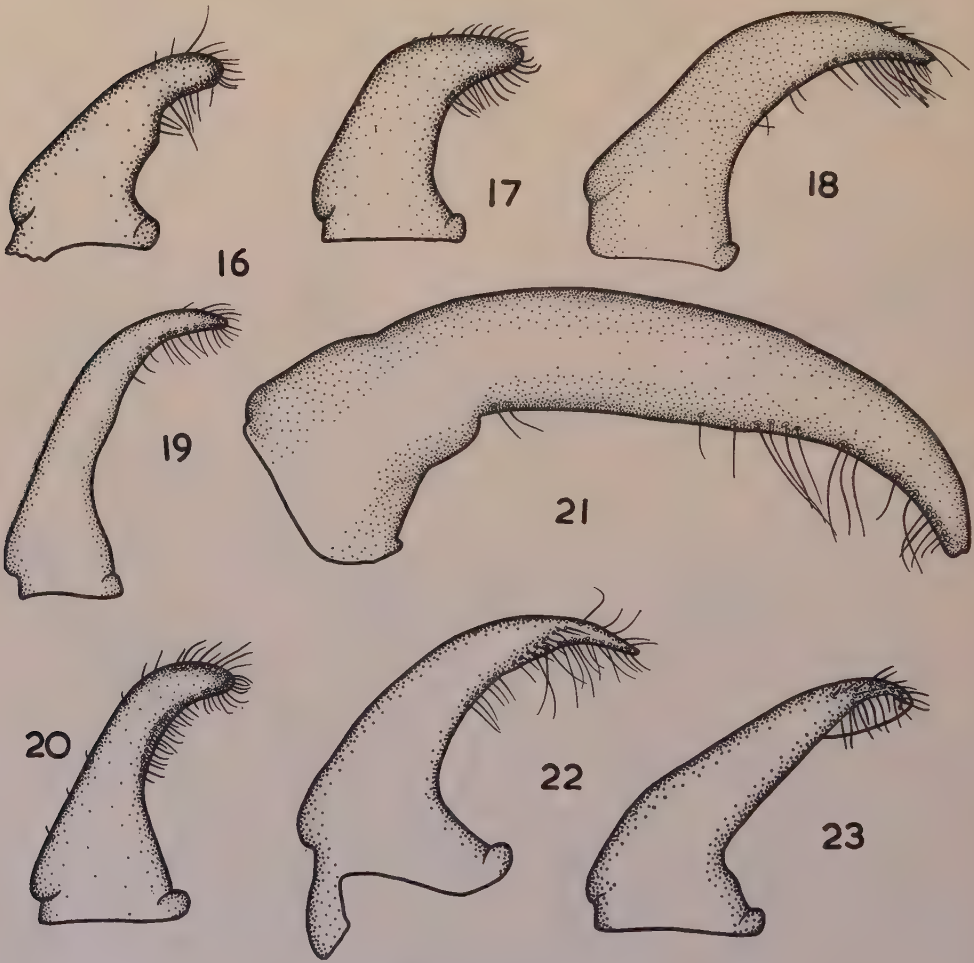
Figs. 10–15.—Lateral lobe of aedeagus, lateral aspect: (10) *C. humeralis*; (11) *C. sexpustulatus*; (12) *C. marginellus*; (13) *C. hemipterus*; (14) *C. flavipes*; (15) *C. obsoletus*.

13 (14) Disc of mesosternum separated from sides by a carina extending diagonally from each side of tip of prosternal process to middle coxae, and often completely or incompletely divided into two cells by a median longitudinal carina. .... (15)

14 (13) Disc of mesosternum not separated from sides by lateral carinae, and median longitudinal carina absent. .... (27)

15 (16) Species dark brown to black with conspicuous humeral and apical yellow or reddish-yellow patches on each elytron. Male with supplementary segment much broader than distance between hind coxae. Female with apex of abdomen truncate, apical fourth of pygidium sharply depressed, and a low broad gibbosity immediately before the depressed area. ...... *C. hemipterus* (L.) (figs. 13 & 28)

16 (15) Elytra without sharply defined lighter areas, more or less unicolorous. (In *C. obsoletus* Er. the humeri are sometimes slightly and diffusely reddish.) .... (17)



Figs. 16–23.—Lateral lobe of aedeagus, lateral aspect: (16) *C. dimidiatus*; (17) *C. maculatus*; (18) *C. davidsoni*; (19) *C. fumatus*; (20) *C. mutilatus*; (21) *C. pallipennis*; (22) *C. niger*; (23) *C. ligneus*.

17 (18) Species obovate with pronotum strongly transverse and base much broader than apex (fig. 2). Last sternite of male with a depressed line running parallel and close to the apical emargination, isolating a narrow transversely alutaceous band from the disc of the sternite. In female, tip of abdomen rounded and apex of pygidium depressed. .... *C. flavipes* Murr. (figs. 14 & 29)

18 (17) Species subparallel, pronotum not conspicuously transverse and base not much broader than apex (fig. 4). Male with supplementary segment about equal in diameter to distance between posterior coxae, and tip of pygidium prominent and upturned. Female with apex of pygidium slightly elevated and tip of abdomen slightly truncate. .... *C. obsoletus* Er. (figs. 15, 30 & 37)

19 (20) Prosternum and hypomeron everywhere coarsely and densely punctured, surface between punctures smooth and shining. Second segment of antennae distinctly shorter than third (fig. 8). .... *C. dimidiatus* (F.) (figs. 16, 31 & 38)

20 (19) Hypomeron almost unpunctured but with small raised granules. Second and third segments of antennae about equal in length (fig. 9). ...... (21)

21 (22) Sides of prosternum almost unpunctured. Disc punctured immediately anterior to process but punctate area not usually extending to anterior margin of prosternum. Hypomeron unpunctured but with small raised granules. Surface everywhere reticulately alutaceous .... (23)

22 (21) Sides and disc of prosternum before process densely punctured, punctures becoming larger and shallower towards the sides, and punctate area extending to anterior margin. Hypomeron impunctate but with raised granules, surface between reticulately alutaceous. .... (25)

23 (24) Punctures on disc of pronotum rather fine and separated near mid-line by a little more than own diameter. Lateral margins of prothorax almost straight between apical and basal angles. Caudal marginal line of mesocoxal cavity meeting metepisternum at about anterior third. ...... *C. maculatus* Murr. (figs. 17 & 32)

24 (23) Punctures on disc of pronotum rather coarse and separated on mid-line by about one diameter or less. Lateral margins of prothorax rather curved between apical and basal angles when viewed from above. Caudal marginal line of mesocoxal cavity approaching metepisternum at about anterior fourth and then diverging posteriorly so as to run parallel to its margin and become obsolete at about its mid-point .... *C. davidsoni* Dobson (figs. 18 & 33)

25 (26) Both sexes with a small gibbosity at the inner base of the hind femur, this is rather inconspicuous in the female but is well developed in the male (fig. 40). .... *C. fumatus* Boheman (fig. 19)

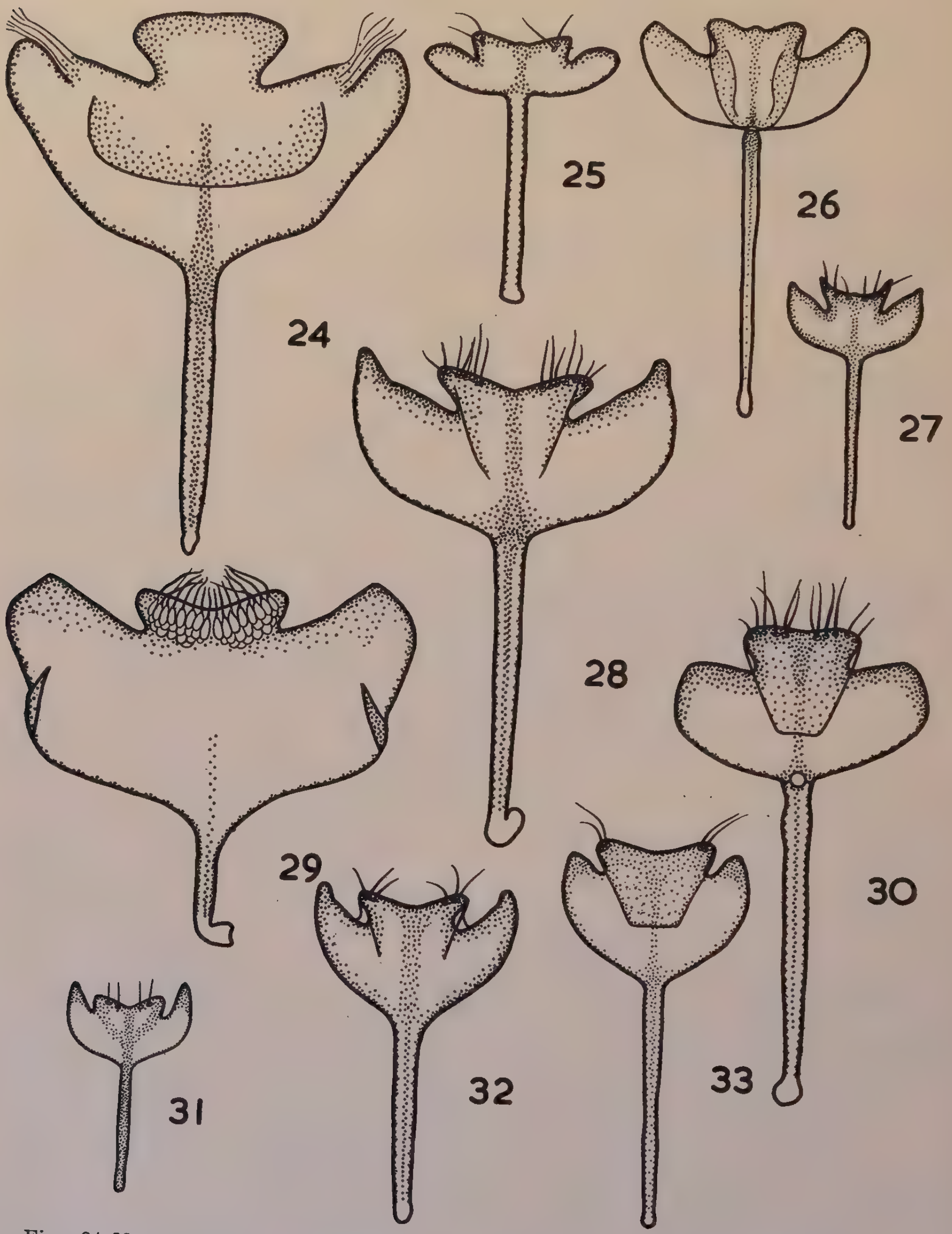
26 (25) No trace of a small gibbosity at the inner base of the hind femur in either sex (fig. 41). .... *C. mutilatus* Er. (figs. 20 & 39)

27 (28) Sides of pronotum evenly rounded into base with basal angles not at all produced. Elytra unicolorous and lighter than rest of body. Female with a prominent tubercle before the apex of the pygidium, and male with supplementary segment terminal and readily visible from above, and with a deep transverse oval pit immediately before apical margin of last sternite. .... *C. pallipennis* (Say) (figs. 21 & 34)

28 (27) Basal angles of pronotum always produced into a point. 29

29 (30) Sides of prothorax evenly curved from apical to basal angles and base of pronotum between angles as broad as base of elytra. Apex of pronotum moderately emarginate. Large black species often with lateral margins of pronotum reddish. ...... *C. niger* (Say) (figs. 22 & 35)

30 (39) Sides of prothorax sinuate before basal angles and base between angles considerably narrower than base of elytra. Apex of pronotum truncate.
C. ligneus Murr. (figs. 23 & 36).

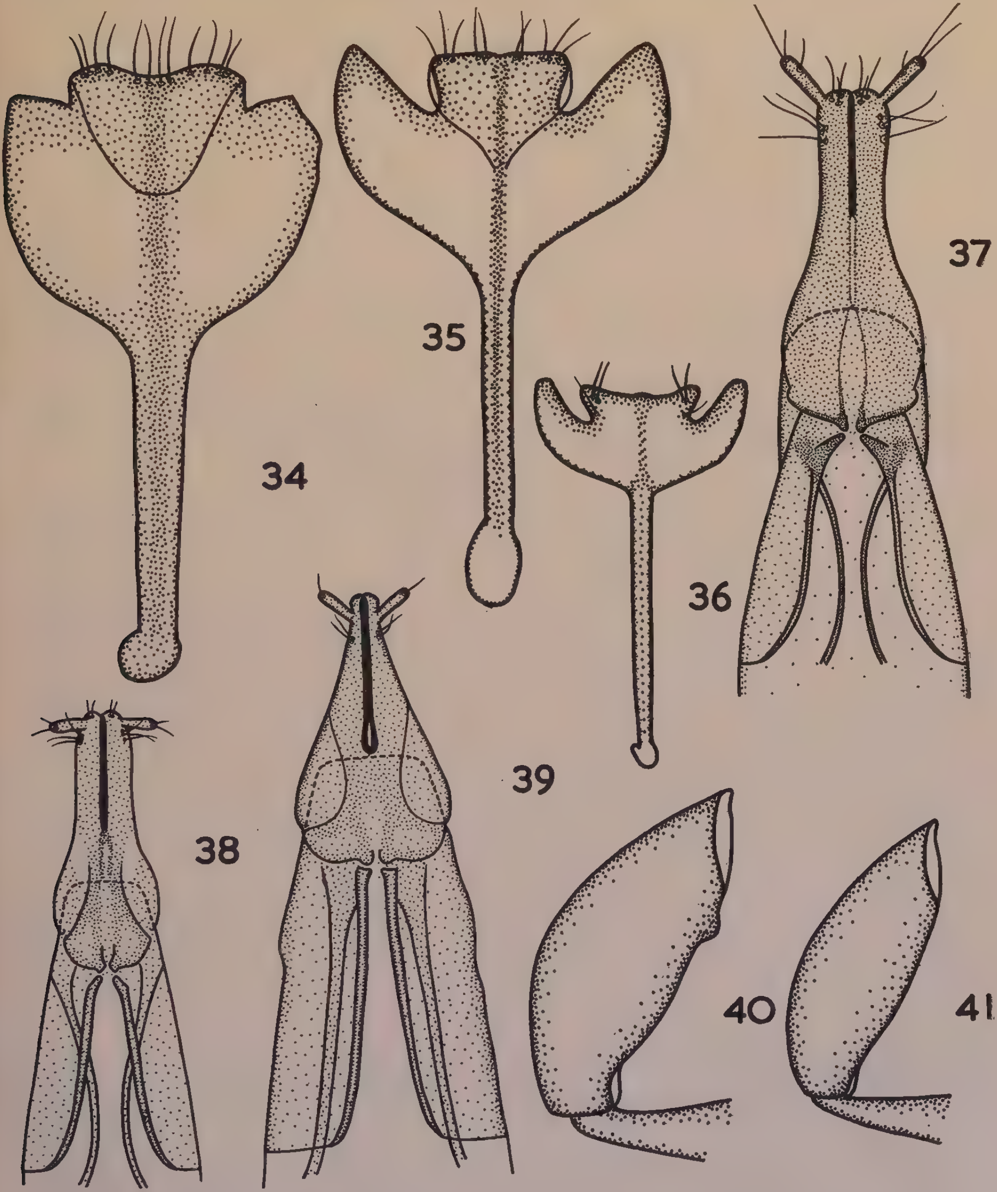


Figs. 24–33.—8th sternite of abdomen of male *Carpophilus* species, ventral aspect: (24) *C. humeralis*; (25) *C. sexpustulatus*; (26) *C. marginellus*; (27) *C. succisus*; (28) *C. hemipterus*; (29) *C. flavipes*; (30) *C. obsoletus*; (31) *C. dimidiatus*; (32) *C. maculatus*; (33) *C. davidsoni*.

Redescription of Some Species.

C. nitidus Murr.

Adult Female.—Broad, convex, obovate, shining castaneous brown to black except for legs which are flavo-testaceous and antennae which are ferrugineous with club darker. Three tergites normally visible posterior to elytra. Pronotum



Figs. 34–36.—8th sternite of abdomen of male *Carpophilus* species, ventral aspect: (34) *C. pallipennis* (damaged specimen); (35) *C. niger*; (36) *C. ligneus*.

Figs. 37–39.—Female genitalia of *Carpophilus* species, ventral aspect: (37) *C. obsoletus*; (38) *C. dimidiatus*; (39) *C. mutilatus*.

Figs. 40–41.—Hind femur of male: (40) *C. fumatus*; (41) *C. mutilatus*.

and elytra almost glabrous, elsewhere sparse pubescence. Length 3–4 mm., breadth 1·8–2·4 mm.

Head.—Strongly punctured. Punctures progressively coarser and denser from clypeus to occiput.

Pronotum.—Transverse with base much broader than apex and slightly sinuate before scutellum. Apex moderately emarginated and greatest breadth at mid-point between apex and base. Sides broadly rounded and laterally of almost uniform thickness, not abruptly thickened towards the apex. Basal and apical angles obtuse and not produced. Discal punctures round, separated by two to three diameters. Peripheral punctures coarser and denser, the largest occurring within the indistinct foveae just before the basal angles. Surface between punctures smooth and shining.

Scutellum.—Rounded-triangular, anterior half finely and sparsely punctured, no lateral impression.

Elytra.—Conjointly much broader than long, greatest breadth just behind midpoint. Base as broad as that of pronotum; humeri not well developed. Near the base punctures are round to oval, slightly coarser than on pronotal disc and separated by about two diameters. Towards suture, apex and sides, punctures much finer and a little closer together. Surface slightly alutaceous on disc and smooth and shining at sides.

Prosternum.—Discal punctures shallow and oval, more than twice as large as eye facets and less than one diameter apart. Process with sides strongly bordered between coxae, tip broadened and punctures half as large as those of disc. Apical half of hypomeron transversely rugose.

Mesosternum.—Carinate laterally, no median longitudinal carina.

Metasternum.—Discal punctures half as large as eye facets and from three to six diameters apart. Lateral punctures three times as large as discal and separated by up to three diameters.

Abdomen.—In dried specimens the two apical segments are retracted into the first segment exposed behind the apex of the elytra. Apex of pygidium sharply deflexed and strongly impressed on each side of the midline so that apparently a pair of lateral and a single median gibbosity are present. Tergal punctures oval, slightly larger than eye facets and more than one diameter apart. Surface between punctures finely alutaceous.

Ventral surface with punctures which are very fine on the disc of each sternite and are three to four times as coarse laterally. A small area of the first sternite is isolated by a raised line running from the lateral corner of the metacoxal cavity to the caudo-lateral corner of the sternite. Surface between punctures finely alutaceous.

Adult Male.—Externally similar to female except that last sternite has a very large median circular depression. There is a stiff brush of erect setae on either side of this ventral depression on the segment immediately preceding it. The supplementary tergite is terminal and cap-like.

C. succisus Er.

Adult Female.—Subparallel, rather depressed. Dorsal surface with scanty and short recumbent golden pubescence. Cuticle castaneous-brown; labrum, legs and antennae except for club lighter. Length 2·3 to 2·6 mm., breadth 1·1 to 1·3 mm.

Head.—Strongly punctate, surface between punctures alutaceous. Clypeal punctures small and round, vertical punctures larger, oval, equal in length to two eye facets and separated by their own length longitudinally and twice their own breadth laterally. At sides between and behind eyes punctures are coarser and denser than on vertex. There is an obscure transverse impression on each side of the head between the antennal insertions. Antennae with first joint strongly dilated anteriorly and joints two and three equal in length. Gula between antennal grooves with shallow round punctures almost twice as large as eye facets and a little more than their own diameter apart. Gula impunctate posterior to antennal grooves.

Pronotum.—Transverse, length to breadth as 1 to 1·6. Rather depressed so that broad lateral margins are observable in dorsal aspect. Sides evenly arcuate, greatest breadth a little behind mid-point. Apex sinuate with rounded but somewhat prominent angles and base slightly sinuate, almost truncate; its angles being obtusely rounded but distinct. Surface punctate except for a median basal strip, discal punctures transversely elongate but not variolose and equal in length to two eye facets. Lateral punctures variolose, progressively coarser and denser until near lateral margin surface is almost rugose. Punctures oriented with longer axes perpendicular to a line drawn from them to a median point at the caudal end of the impunctate strip, towards which point the scanty pubescence is directed. Surface between punctures coarsely alutaceous.

Scutellum.—Shining and alutaceous. Punctured on anterior two-thirds and with lateral impressed line on anterior third.

Elytra.—Subparallel with greatest breadth about mid-point between apex and base. Suture from apex to scutellum slightly longer than pronotum along its mid-line, 1·16 to 1·0. Surface everywhere coarsely alutaceous with oval to irregular punctures twice as coarse as eye facets and separated by a little more than their own diameter near base. Punctures become progressively smaller towards apex where they are separated by about twice their own diameter. Punctures immediately flanking suture round and smaller than those of disc.

Prosternum.—Process impunctate and subcarinate with margins moderately raised and thickened between coxae so that together they account for about half its total width at this point. Prosternal disc anterior to process punctured except on apical third, punctures deep, round, slightly larger than eye facets and less than one diameter apart. Towards sides punctures larger, shallower and denser. Surface between lateral punctures faintly alutaceous. Hypomeron impunctate but bearing raised granules which are finer than eye facets and are separated by almost twice their own diameter. Surface between moderately alutaceous.

Mesosternum.—Punctate on disc only. Punctures oval, slightly coarser than those of prosternal disc and separated by less than half a diameter. Neither median nor lateral carinae present.

Metasternum.—Discal punctures small, round and from one to five diameters apart. Lateral punctures larger and ill-defined so that surface appears rugose. Caudal marginal line of mesocoxal cavity parallel to cavity along median third and then diverging latero-posteriorly to meet metepisternum asymptotically at its apical third. Axillary area thus defined large, impunctate but shagreened. Median furrow well defined.

Abdomen.—Pygidium rounded apically, slightly emarginate laterally and depressed discally. Surface with fine setiferous granules. Hypopygidium evenly curved at apex and sculptured like pygidium.

Adult Male.—Externally similar to female except that median portion of last sternite is emarginated to about half its depth to accommodate supplementary tergite. Tergite preceding supplementary rather more acuminate than corresponding one in female, not emarginate at sides and slightly elevated at the extreme apex.

C. mutilatus Er.

Adult Female.—Subparallel, moderately convex. Dark to pale ferrugineous brown, moderately shining. Elytra usually paler than remainder except for suture, apex, sides and sometimes scutellar region dark. Pronotum usually darker on mid-line than at sides. Dorsal surface with moderate recumbent to suberect pubescence which is golden except at apical sides of elytra where it is black. Length 2·3–3·3 mm., breadth, 0·9–1·5 mm.

Head.—Punctures of clypeus small and round, those of vertex larger, equal to two eye facets, variolose and one diameter apart. Occipital punctures round, almost contiguous and less than those of vertex. Antennae paler than head, second segment equal to third in length. Gula between antennal grooves with round shallow punctures twice as large as eye facets and very close together. Behind antennal grooves gula impunctate, smooth and shining.

Pronotum.—Moderately transverse (length to breadth 1 to 1·5). Greatest breadth just before basal angles. Apex truncate, angles evenly rounded not prominent. Base shallowly bisinuate, angles obtuse. Surface everywhere strongly alutaceous and except for a variable median strip punctured. Discal punctures variolose, a little larger than eye facets and separated by slightly more than one diameter. Lateral punctures coarser and denser. Emarginated lip of punctures directed towards margin of pronotum, axis of orientation being at a point on mid-line at basal fourth. The pubescence is directed towards this point.

Scutellum.—Alutaceous, anterior half strongly punctured and with a lateral impressed line.

Elytra.—Subparallel, broadest at apical third and equal in breadth at base to base of pronotum. Suture from scutellum to apex about equal in length to pronotum. Punctures near scutellum round to irregular, equal to those at sides of pronotum. Laterally and apically punctures much smaller and more than two diameters apart. Surface between punctures coarsely alutaceous.

Prosternum.—Margins of process between coxae strongly raised, together accounting for more than half its breadth. Surface punctured, moderately convex but not carinate. Disc with deep, round to irregular punctures which are coarser than eye facets and less than one diameter apart. Lateral punctures larger and shallower. Surface between punctures smooth and shining. Hypomeron impunctate but with raised granules about as large as eye facets and more than one diameter apart. Surface between granules alutaceous.

Mesosternum.—Discal punctures round, coarser than those of prosternal disc and very dense. Towards sides punctures become ill-defined and lateral third is impunctate. A variable median unpunctured strip sometimes appears slightly carinate.

Metasternum.—Discal punctures equal to or slightly larger than eye facets and separated by almost two diameters. Lateral punctures larger, longitudinally elongated and deeper at apex than at base. Caudal marginal line of mesocoxal cavity parallel to cavity along its mesal two-thirds and then diverging posteriorly so as to meet metepisternum at a point about half-way between its apex and base. Axillary area impunctate.

Abdomen.—Dorsal and ventral surfaces reticulately alutaceous. Discal punctures of first sternite round, much smaller than those of metasternal disc and separated by about two diameters. Behind posterior coxae, surface impunctate but granular. Hypopygidium evenly curved apically, and with setiferous granules anterior to the indistinct oval punctures. Pygidium flattened, slightly emarginate at sides and evenly rounded at apex. Sculptured similarly to hypopygidium.

Adult Male.—Externally similar to female except that the median portion of the last sternite is emarginated to about half its depth to accommodate the supplementary tergite. Tergite preceding supplementary not emarginate at sides. Prothorax more parallel-sided than in female.

C. fumatus Boheman.

This species resembles *C. mutilatus* Er. so closely that a separate detailed description is scarcely justifiable. The only well-marked external feature which serves to separate the two species is a small gibbosity at the inner base of the hind femur which is present in both sexes of *C. fumatus* Boh. (fig. 40) but is absent in *C. mutilatus* Er. (fig. 41). The presence of this gibbosity in the female is best determined by examining the detached leg under a moderately high power magnification.

In the male as the gibbosity is proportionately much larger and is often dark-pigmented there should be no need to remove the leg.

The male genitalia of the two species (figs. 19 & 20) may readily be distinguished.

The Importation of *Carpophilus* spp. into Britain on Stored Products during Recent Years.

The following Table has been compiled from the records of numerous Inspectors of the Infestation Control of the Department of Agriculture for Scotland and the Infestation Control Division of the Ministry of Agriculture and Fisheries during the period 1943–1950 in Scotland and 1948–1950 in England and Wales.

Difficulty was experienced in determining the criteria upon which the accuracy of identification might be judged. Whenever possible representative specimens have been examined, but in the many cases where this proved to be impossible only identifications checked at the British Museum (Nat. Hist.) were acceptable as reliable. Attention is drawn in the Table to any record which was not confirmed.

The Table provides information concerning the occurrence and distribution of the various species and the range of commodities infested.

TABLE I.

Recent records of *Carpophilus* species imported into Britain on stored produce.

Species	Commodity	Place of origin	Port of shipment	Number of records	Additional information
Carpophilus mutilatus	Dates	Iraq	Basra	1	
	,,	,,	unknown	1	
	Copra	Philippine Islands	unknown	1	
Carpophilus maculatus	Copra	Philippine Islands	Zamboanga & Cebu	1	
	,,	,,	unknown	1	
	,,	Ceylon	Colombo	1	
	,,	,,	unknown	1	
Carpophilus succisus	Maize	Brazil	unknown	1	
Carpophilus humeralis	Copra	Far East	unknown	1	
	Onions	unknown	unknown	1	
Carpophilus nitidus	Dried bananas	West Africa	unknown	1	
Carpophilus hemipterus	Dates	Iraq	Basra	1	
	,,	,,	unknown	13	Ten records not confirmed but probably correct

Species	Commodity	Place of origin	Port of shipment	Number of records	Additional information
Carpophilus hemipterus	Dates	unknown	unknown	2	
	Figs	Iraq	unknown	1	
	,,	unknown	unknown	1	
	Sultanas	Turkey	Smyrna	1	Not confirmed
	,,	unknown	unknown	2	
	Apricots, fruit salad and prunes	South Africa	unknown	1	Not confirmed
	Mixed peel	West Indies	unknown	1	
	Cocoa beans	Fiji & Samoa	Suva, Rotumah, Levuka, Apia	1	
	,,	West Africa	unknown	1	
	,,	West Indies	unknown	1	
	Copra	Ceylon	Colombo	1	
	,,	Fiji & Samoa	Suva, Rotumah, Levuka, Apia	1	
	Groundnuts	India	Bombay	1	
	Linseed	India	Bombay	1	Not confirmed
	Barley	Argentine	River Plate port	1	Living on barley stored in London warehouse for eighteen months
	Wheat	U.S.A.	Baltimore	1	On U.S.A. No. 2 Red Winter Wheat
	Flour	U.S.A.	New Orleans	1	
	Onions	Egypt	Alexandria	1	
	,,	unknown	unknown	1	
Carpophilus dimidiatus	Cocoa beans	West Africa	unknown	7	
	,,	West Africa (Gold Coast)	unknown	1	
	,,	West Indies	unknown	2	One not confirmed
	,,	,,	Grenada	2	
	,,	Fiji & Samoa	Suva, Rotumah, Levuka, Apia	1	
	,,	unknown	unknown	3	
	Groundnuts	India	Madras	2	
	,,	,,	Calcutta	1	Not confirmed
	,,	,,	Navlaklie	1	Not confirmed
	,,	,,	Bedi-Bunder	1	Not confirmed
	,,	,,	Marmagao	1	Not confirmed
	,,	,,	unknown	1	Not confirmed
	,,	West Africa	Lagos	4	One not confirmed
	,,	,,	Freetown	1	Not confirmed
	,,	,,	Burutu	1	
	,,	,,	Gambia river	1	
	,,	,,	Dakar	1	Not confirmed
	,,	,,	unknown	3	One not confirmed. In one case breeding in warehouse one year after importation
	,,	unknown	unknown	1	Not confirmed
	Palm kernels	West Africa	Freetown	3	Two not confirmed
	,,	,,	Lagos	3	One not confirmed
	,,	,,	Burutu	1	
	,,	,,	Gambia river	1	

Species	Commodity	Place of origin	Port of shipment	Number of records	Additional information
Carpophilus dimidiatus	Palm kernels	West Africa	Takoradi	1	
	„	Malaya	unknown	1	
	„	unknown	unknown	1	
	Copra	Tonga Is., Fiji & Samoa	Suva, Rotumah, Levuka, Apia	3	
	„	Philippines	Nukualopa	1	
	„	Ceylon	Colombo	2	One not confirmed
	„	West Africa	Lagos	1	
	„	„	Takoradi	1	
	Nutmegs	West Indies	Grenada	1	
	„	„	Trinidad	2	One not confirmed
	„	„	unknown	3	Two not confirmed
	„	South America	Demerara	1	Not confirmed
	Linseed	India	Calcutta	1	Not confirmed
	„	„	Karachi	1	Not confirmed
	Myrabollams	„	Calcutta	1	
	Rice	Burma	Rangoon	1	
	„	„	unknown	1	
	„	Brazil	unknown	1	
	Maize meal	East Africa	Mombasa	1	
	Cotton seed	South & East Africa	unknown	3	One not confirmed and one possibly cross-infestation from other commodity in same ship
	Coffee beans	East Africa	unknown	1	May have been cross-infestation from above cotton seed
	Mace	West Indies South America	Trinidad Demerara	2	Not confirmed
	Dates	Iraq	unknown	5	Four not confirmed
	Currants	Australia	unknown	1	Not confirmed
	Almond kernels	Sicily	Catania	1	
	Brazil nuts	unknown	unknown	1	
	Soya beans	Brazil	Rio Grande	1	
	Oil-cakes	East Africa	unknown	1	
	(Flour mill,	London)		(1)	(In screen section of flour mill)
Carpophilus marginellus	Cocoa beans	West Africa	unknown, but Gold Coast	1	
	Wheat	U.S.A.	Baltimore	1	On No. 2 Red Winter Wheat
Carpophilus obsoletus	Dates	Iraq	Basra	1	
	„	„	unknown	2	
	„	unknown	unknown	1	
	Figs	unknown	unknown	1	
	Mixed peel	West Indies	unknown	1	
	Copra	Ceylon	Colombo	1	
	„	„	unknown	2	
	„	West Africa	Lagos	1	
	„	„	Takoradi	1	
	„	Philippines	Apia	1	
	Palm kernels	West Africa	unknown	1	

Species	Commodity	Place of origin	Port of shipment	Number of records	Additional information
Carpophilus obsoletus	Palm kernels	West Africa	Lagos	2	
	"	"	Freetown	1	
	"	"	Takoradi	1	
	"	Malaya	unknown	1	
	Cocoa beans	West Africa	Freetown	1	
	"	"	unknown	3	
	Groundnuts	West Africa	Lagos	2	
	"	"	Freetown	1	
	"	"	unknown	1	
	Onions	Egypt	Alexandria	1	
	"	unknown	unknown	1	
	Lonchocarpus root	South America	unknown	1	
	Candied peel	West Indies	Jamaica	1	
Carpophilus ligneus	Cocoa beans	West Africa	unknown	1	Breeding three years after importation
	Candied peel	unknown	unknown	1	Possibly cross-infestation from Smyrna sultanas
	Sultanas	Turkey	Smyrna	1	
	Raisins	South Africa	Capetown(?)	1	
	Currants	Greece	unknown	1	
	Figs	Iraq	unknown	1	
	"	unknown	unknown	1	

Acknowledgements.

I am grateful to Dr. D. W. Williams, Principal Scientific Officer of the Infestation Control of the Department of Agriculture for Scotland who provided facilities enabling me to carry out the work. I thank Dr. J. A. Freeman, Principal Scientific Officer of the Infestation Division, Ministry of Agriculture and Fisheries, for arranging that material be sent to me for identification and study. I also thank Professor H. W. Miles, Professor O. W. Richards, Dr. H. E. Hinton and Mr. R. G. Davies for valued assistance.

Summary.

Sixteen of the numerous described species of *Carpophilus* Stephens have been found associated with stored products in different parts of the world, and of these, several species are continually distributed by international trade and have become established in many countries.

A key to most of these species is given, several of the species are redescribed and new taxonomic characters, mainly associated with the genitalia, are introduced and figured.

A Table is given summarising recent importations of *Carpophilus* species into Britain, detailing the commodities on which the insects have been found, their places of origin and the number of individual records.

References.

Dobson, R. M. (1952). Ent. mon. Mag., **88,** pp. 256–258.

Fowler, W. W. (1889). The Coleoptera of the British Islands, **3,** London.

Hinton, H. E. (1945). A monograph of the beetles associated with stored products, **1,** London, Brit. Mus. (Nat. Hist.).

TOXICITY OF THE BOTANICAL INSECTICIDE *RYANIA SPECIOSA* TO *CULEX PIPIENS FATIGANS* WIED.*

By L. J. Charles, M.B., Ch.B.(Edin.).
Chief Officer, Mosquito Control Service,
Medical Department, British Guiana.

Ryania speciosa, a small shrub belonging to the Family Samydaceae, is indigenous to northern South America and parts of the West Indies, and attains a height of 10–15 feet with stems of half to one inch diameter. It was known to occur gregariously in British Guiana on the Pomeroon, Essequibo and Mazaruni rivers and local attention was directed to it in 1949 by commercial enquiries from the United States of America.

Heal (1949) reported that in the course of a research programme directed towards a survey of insecticidal properties in materials of botanical origin, *Ryania speciosa* was shown in 1943 to possess high insecticidal activity against certain insect species and that, in experiments under field conditions made at the New Jersey Agricultural Experiment Station, the ground root of this shrub proved effective against *Pyrausta nubilalis* (Hb.) (the European corn borer). Later reports by Dugas and Concienne (1947) demonstrated control of *Diatraea saccharalis* (F.) (the sugar-cane borer) by means of *Ryania* dusts; Carruth and Hervey (1947) reported on its activity against *Melittia cucurbitae* (Harr.) (the squash borer); and Dills and Odland (1948) observed good results against the cabbage caterpillar (*Pieris rapae* (L.)). During 1947 and 1948 Apple and Decker (1950), studying the effects of concentrated insecticide sprays against *P. nubilalis* recorded very erratic results with *Ryania* extractives in oil and water solutions, and in emulsion.

In his review of the agricultural trials with *Ryania*, Heal (1949) reported that neither pulverised stem used as dust or aqueous suspension, nor certain crude *Ryania* extractives showed significant activity against *Aëdes aegypti* (L.), and a dosage of 10 parts per million of the active principle ryanodine was required for LD50 against 3-day-old *aegypti* larvae. This alkaloid was soluble in, and extractable from the stem with water, alcohol and other solvents.

By the end of 1951, British Guiana had achieved successful eradication of the mosquito vectors of malaria and urban yellow fever from the populated coastlands by means of residual DDT (Giglioli, 1951; Charles, 1953*a*), but the important problem of Bancroftial filariasis and its classical vector *Culex pipiens fatigans* Wied. remained largely unsolved. This latter mosquito species was still prevalent and constituted over 98 per cent. of house-caught adult mosquitos collected during routine surveys made in 1950–52 in the coastal towns and villages. It appeared to be unamenable to control solely by residual insecticidal application, and indications were that larvicidal measures would need to be incorporated in any concerted effort directed towards its abatement. Waterlogged pit latrines common in the villages constituted important production foci of this species (Charles, 1953*b*).

In the course of investigations on control of this vector it was natural that a reputed insecticidal plant occurring locally should be given due consideration, and this report summarises the results of laboratory observations made during 1951–52 on the toxicity of *Ryania speciosa* to larvae and adults of *Culex pipiens fatigans*.

---

* This paper is submitted with the kind permission of the Director of Medical Services, British Guiana.

Methods and Materials.

Supplies of young dried stems of *Ryania speciosa* approximately one inch in diameter were obtained from the Department of Local Government. Previous analysis of a local sample had shown it to contain 0·4 per cent. crude ryanodine* and an aqueous extract was made by soaking 370 gm. of finely chipped dried *Ryania* stem in 1,800 ml. cold rain water for 48 hours, when the sherry-coloured liquid was drained off and the loss from absorption made up with small washings poured over the chips. This stock extract, with a pH of 6·8, and later reported* to contain 17·4 mg. crude ryanodine per 100 ml., was employed in 100 ml. lots of varying dilution against 12-hour-old first-instar larvae of *C. pipiens fatigans*. Each lot was fed daily with a standard quantity of brewers' yeast and the loss by evaporation at room temperature (approx. 85°F.) was made up every 24 hours with rain water, the mean from four control vessels being taken as the daily loss.

Each day larval counts were made, dead specimens being removed with a dissecting needle. Surviving pupae were allowed to emerge under a mosquito net. Five replicates of each dilution were employed, with controls, and each experiment was repeated 3–5 times. Additional control runs were made in the first experiment with a comparable aqueous extract of guava stem (*Psidium guajava*).

After initial use of the above *Ryania* extract, the proportionate weights of chipped *Ryania* stem were added to 100 ml. rain water in small enamel bowls, some of which were daubed with a mixture of mud and cowdung. Replenishment of daily loss and larval feeding was maintained, but larval counts were not practicable because frequent emptying of the dishes led to disintegration of the mud layer. Adult emergence was readily determined, however, from pupal cases floating on the surface, and from their number larval mortality was computed.

Larvae used were of two types, a " Colony " strain from an 18-month-old laboratory colony, and a " New Town " strain reared in the laboratory from gravid house-caught females newly captured at a suburban village.

For adult exposures, aqueous and 70 per cent. alcoholic extracts of *Ryania* were prepared as above, and 100 ml. of each preparation was applied evenly with a pipette and allowed to dry on painted and unpainted 6-inch squares of board. Two-day-old honey-fed female *C. pipiens fatigans* were exposed to treated and control squares under 3-inch diameter glass funnels for two hours, transferred to observation cages, and their percentage mortality noted after 24 and 48 hours. Transference to and from the squares was facilitated by anaesthetisation with carbon dioxide gas from a commercial cylinder. " New Town " adults were reared from pupae collected in a pit latrine.

Results.

Experiment 1.

This experiment was set up to determine the existence of any larvicidal action by *Ryania*. Waxed ice-cream cups were used, and extract of guava stem was used for comparison. The results with 100 first-instar " Colony " larvae are shown in Table I. All larvae in the *Ryania* cups died within 48 hours, while in the guava and controls the greater majority pupated and emerged within ten days. Similar results were obtained with second-, third-, and fourth-instar larvae, although in the 1 : 3 dilution second and third instars died only after three and four days, respectively, while fourth instars survived for six days in the stock and seven days in the other two dilutions before they all died.

Experiment 2.

The *Ryania* cups and extracts employed in Experiment 1 were used, after an interval of 16 days, to determine the maximum duration of the toxic effects

---

* All analyses for ryanodine were made by Messrs. Seil, Putt & Rusby, Inc. of New York.

TABLE I.

Comparative toxicity of aqueous extracts of *Ryania* and guava to first-instar larvae of *C. pipiens fatigans* (" Colony " strain).

Dilution	No. larvae exposed	*Ryania*			Guava			Control		
		Per cent.			Per cent.			Per cent.		
		Larvae died	Pupated	Emerged	Larvae died	Pupated	Emerged	Larvae died	Pupated	Emerged
Stock	100	100·0	0	0	6	94	94·0	1·0	99·0	99·0
1 : 1	100	100·0	0	0	3	97	97·0	—	—	—
1 : 3	100	100·0	0	0	8	92	92·0	—	—	—

observed. First-instar "Colony" *C. pipiens fatigans* larvae were introduced at the end of this and two subsequent 16-day intervals in each of ten cups with the results shown in Table II. There was evidence of loss of toxicity after the first 16-day interval which was more pronounced after a second and equal period. By the end of this latter period, further observations were rendered impracticable by the appearance of a dense surface mould on the solutions.

TABLE II.

Deterioration of the larvicidal action of an aqueous extract of *Ryania speciosa* at 16-day intervals.

Ryania dilution	Larvae exposed	Exposures— % larval mortality		
		1st	2nd	3rd
Stock* ..	100	100·0	96·0	80·0
1 : 1 ..	100	100·0	90·0	62·0
1 : 3 ..	100	100·0	57·0	21·0

* 17·8 mg./100 ml. crude ryanodine.

Experiment 3.

This experiment was originally planned to determine the toxicity of *Ryania* to larvae of *C. pipiens fatigans* occurring under natural conditions, and "New Town" larvae as described above were employed. Because a substantial difference in anticipated results was observed, parallel series of "Colony" and "New Town" larvae were set up, and with a view further to emphasise these differences higher dilutions of *Ryania* extract were included.

Since all survivors pupated and the greater majority of these emerged, the results summarised in Table III, show only larval mortalities. Although total kills of "Colony" first instars were not obtained with comparable concentrations

TABLE III.

Comparative toxicity of an aqueous extract of *Ryania speciosa* to first-instar larvae of two strains of *C. pipiens fatigans*.

Dilution	No. larvae exposed	% Larval mortality in *C. pipiens fatigans* strains	
		"Colony"	"New Town"
Stock ..	250	100·0	98·0
1 : 1 ..	250	98·4	87·3
1 : 3 ..	250	93·3	70·6
1 : 7 ..	150	62·0	39·4
1 : 15 ..	150	36·0	22·0
Control ..	200	1·5	1·0

as in Tables I and II, the toxicity of *Ryania* to *C. pipiens fatigans* larvae was confirmed, and there was a consistent and significant lower mortality of " New Town " larvae in all dilutions of the same aqueous extract.

Experiment 4.

Enamel bowls were heavily lined with a mixture of mud and cowdung, both selected against possible contamination with synthetic insecticides, and 20·5 and 10·25 gm. respectively chipped *Ryania* stem was added to 100 ml. rain water, which, after 48 hours, would provide a concentration equivalent to *Ryania* stock infusion and 1 : 1 dilution as employed in the preceding observations. Controls were run both in daubed bowls and in plain bowls, with and without *Ryania* chips. All bowls were used for exposure of a second batch of larvae after a 16-day interval, but their use for further exposures was made impracticable by virtue of disintegration of the mud linings.

In the first exposure, " Colony " larval kills (80 per cent.) were lower in the daubed bowls than in corresponding plain bowls (100 per cent.) and although total kills were not obtained with " New Town " larvae in plain bowls, mortality rates were significantly lower also in the corresponding daubed vessels (Table IV).

TABLE IV.

Toxicity of *Ryania* to first-instar larvae of two strains of *C. pipiens fatigans* in the presence of extraneous organic matter.

Test conditions		No. larvae exposed	Per cent. larval mortality			
			First exposure		Second exposure	
			" Colony "	" New Town "	" Colony "	" New Town "
Daubed bowls	*Ryania* stock ..	200	84·0	79·0	71·0	61·0
	Ryania 1 : 1 ..	200	80·0	70·0	59·5	35·0
	Control ..	100	4·0	3·0	6·0	3·0
Plain bowls	*Ryania* stock ..	200	100·0	98·0	98·0	84·0
	Ryania 1 : 1 ..	100	100·0	91·0	67·0	70·0
	Control ..	100	1·0	1·0	0·0	0·0

The lower susceptibility of " New Town " larvae recorded in Table III was again observed. The second exposure yielded reduced larval kills throughout, and the differential response by the two strains of *C. pipiens fatigans* was maintained in both of the extract dilutions employed.

Experiment 5.

Adult " Colony " *C. pipiens fatigans* were initially exposed for two hours to wooden squares treated with 100 ml. each of aqueous and alcoholic *Ryania* extract. All observations, made within the first week after treatment of the wooden surfaces, showed that *Ryania* had no toxicity as a contact insecticide against adults of *C. pipiens fatigans* (Table V). Subsequent commercial analysis showed 0·057 per cent. ryanodine content of the alcoholic extracts employed. The ryanodine dosage on the treated surfaces therefore approximated to 71 and 230 mg./sq. foot respectively for the aqueous and alcoholic applications.

TABLE V.

Adult mortality of *C. pipiens fatigans* after two hours contact with *Ryania* extract.

Strain	Per cent. adult mortality								
	Aqueous extract			Alcoholic extract			Control		
	No. exposed	24 hrs.	48 hrs.	No. exposed	24 hrs.	48 hrs.	No. exposed	24 hrs.	48 hrs.
" Colony "	75	0·0	5·3	75	1·3	2·7	40	0·0	0·0
" New Town "	75	0·0	4·0	75	0·0	5·3	40	0·0	5·0

Discussion.

Results of the experiments showed some toxicity of *Ryania* aqueous extract to all larval stages of *C. pipiens fatigans*, since a pH of 6·8, as in the extract employed, was within the tolerance pH range of 1·6–9·6 recorded by Senior White (1934), while the probable toxic effects of other non-specific chemical constituents of the young stem, *e.g.*, tannin, was controlled by the comparable extracts of the guava plant set up in Experiment 1. This latter, with a pH of 6·5 gave relatively small and irregular larval kills (Table I). Although the toxicity of *Ryania* was well sustained for one month in the stock extract under clean conditions, rapid deterioration was recorded in the dilution tested, the larval mortality in a 1 : 3 dilution falling off from 100 to 21 per cent. in 32 days, when further observations became impracticable.

The statistically significant differential larval responses of a protected colonised, and a naturally occurring strain of *C. pipiens fatigans* to *Ryania* was of some interest, for the latter was collected in an area which had been subjected to routine residual DDT applications for six years. It was this observation which prompted analysis of the experimental extracts for crude ryanodine content. Thus, from the data presented in Table III the lethal doses for first-instar larvae of the two strains of *C. pipiens fatigans* could be computed in p.p.m. ryanodine as follows:

Larvae	LD90	LD50
" Colony "	43	17
" New Town "	114	31

Preliminary follow-up of these findings with some of the chlorinated hydrocarbon group of insecticides have indicated comparable differences in larval susceptibility.

Quite apart from the above massive LD50 of ryanodine required for larvae of *C. pipiens fatigans*, the most important results from the practical viewpoint were those summarised in Table IV. Not only was larval mortality appreciably reduced in the presence of organic matter as would be encountered in a pit latrine, but after an interval of 16 days only 35·0 per cent. of first-instar " New Town " larvae were killed by *Ryania* stem at the rate of 20·5 gm./100 ml. water. Although later observations were again impracticable, the progressively lower larval kills obtained after this interval under clean conditions (Table III) appeared to indicate the probable trend in results of further exposures in the simulated pit conditions of Experiment 4. After removing the sticks and draining off the water from two bowls containing stock *Ryania*, analysis of the dried mud showed an average 11·2 mg. crude ryanodine content. Since 100 ml. of stock aqueous extract contained 17·8 mg., it would appear that 62 per cent. of the ryanodine extracted from the sticks in individual bowls was adsorbed by the mud-cowdung mixture, and this probably accounted largely for the initial reduced toxicity observed. This, in conjunction with the tremendous bulk of an equivalent weight of *Ryania* stem (2 lbs./gal.) which would be required for pit latrines, which averaged 127 gallons of water in February 1951, demonstrated the impracticability of utilising unprocessed *Ryania* for larvicidal control of *C. pipiens fatigans*.

As a contact insecticide against adults of this species, *Ryania* appeared to be entirely non-toxic.

Summary.

In the course of general studies on control of *Culex pipiens fatigans* Wied. in British Guiana, the indigenous shrub *Ryania speciosa*, proven to possess insecticidal activity against certain agricultural pests, was investigated.

Aqueous extracts of the dried stem were shown to possess toxic properties against all larval stages of *C. pipiens fatigans* under clean laboratory conditions. Under conditions simulating a water-logged pit latrine, however, toxicity was

greatly reduced by adsorption of the active agent ryanodine, rendering the crude stem relatively ineffective after 16 days. Because of the great bulk of unprocessed material required for even this limited result in pit latrines—which constitute an important local problem—*Ryania* was not considered of practical value in *C. pipiens fatigans* control.

Aqueous and alcoholic extracts of *Ryania speciosa* had no contact insecticidal properties against adults of this species.

References.

Apple, J. W. & Decker, G. C. (1950). Corn Borer control on sweet corn with concentrated sprays.—J. econ. Ent., **43,** pp. 407–414.

Carruth, L. A. & Hervey, G. E. R. (1947). DDT and other insecticides for Squash Borer control.—J. econ. Ent., **40,** pp. 716–721.

Charles, L. J. (1953*a*). Mosquito Control Service, British Guiana. Annual Report 1952.—18 pp., multigraph.

Charles, L. J. (1953*b*). A field experiment in residual control of the adults of *Culex fatigans* in British Guiana.—Ann. trop. Med. Parasit., **47,** pp. 113–125.

Dills, L. E. & Odland, M. L. (1948). Cabbage caterpillar insecticide tests.—J. econ. Ent., **41,** pp. 948–950.

Dugas, A. L. & Concienne, E. J. (1947). Sugar-cane investigations in 1946. Part 1.—Rep. Sugar-cane Contact Comm. Louisiana agric. Exp. Sta.

Gigliolo, G. (1951). Nation-wide malaria eradication projects in the Americas. III. Eradication of *Anopheles darlingi* from the inhabited areas of British Guiana by DDT residual spraying.—J. nat. Malar. Soc., **10,** pp. 142–161.

Heal, R. E. (1949). A new insecticidal material shows promise in preliminary tests. Low toxicity feature of Ryania insecticides.—Agric. Chem., **4,** no. 5 pp. 37, 39, 89, 91.

Senior White, R. (1934). Three years mosquito control work in Calcutta.—Bull. ent. Res., **25,** pp. 551–596.

THE EFFECT OF POISON BAIT CATTLE ON POPULATIONS OF *GLOSSINA MORSITANS* WESTW. AND *G. SWYNNERTONI* AUST.

By G. F. Burnett.

Colonial Insecticide Research Unit, Arusha, Tanganyika.

Whiteside (1949) describes an attempt to control the tsetse, *Glossina pallidipes* Aust., by the use of DDT-treated oxen used as bait. The idea behind this experiment was that if cattle in excess of the natural game hosts were offered to the fly a large proportion of the latter would feed on them and be killed by the insecticide so picked up. The experiment was concluded after five months when the catch of non-teneral females had fallen by 95 per cent. Extermination was calculated to require another seven months and the experiment was not continued.

On the basis of Whiteside's experience it was considered that *G. morsitans* Westw. or *G. swynnertoni* Aust. were more promising species to work on by this method as they come readily to cattle, feed during the day-time when cattle can be conveniently kept in the bush and are less restricted than *G. pallidipes* to feeding on the legs and belly where insecticide is difficult to apply and retain.

Experimental Details.

Site of experiment.

The experiment was carried out in a block of bush known as Gedemara which is situated about nine miles east of Ufiome Mountain (Lat. 04°14′S., Long. 35°47′E.), in the Northern Province, Tanganyika Territory. The block is half a mile square. It was left, at the request of the Colonial Insecticide Research Unit, when clearings were made for native settlement round the mountain in 1949–1950. There is no bush within several miles except to the north and north-east where, at its closest, an area of Combretaceous bush, known as Ghaidoho, containing both species of tsetse, is within one and a half miles of Gedemara block (fig. 1). Between the two, however, is a valley and a ridge and neither is visible from the other. This may reduce the movement of tsetse between the two areas. Between north-east and east there is no such obstruction, but the distance is greater. Here the bush consists of *Acacia spirocarpa* supporting *G. swynnertoni*. The southernmost third of Ghaidoho, between east and south-east, is gall acacia in which a few *G. swynnertoni* are found. Between Gedemara and the acacia is naturally treeless grassy *mbuga* and there appears to be a good deal of game movement, principally zebra and Coke's hartebeest, from or past the acacia woodland towards and into the block. Dik-dik and probably pig are permanent residents in Gedemara, impala and greater kudu live there for weeks at a time and less regular visitors are roan antelope, giraffe, rhinoceros, lion, reedbuck and hyaena. The general relation of the block to Ghaidoho is shown on the map (fig. 1). The latter is indicated only by lettering, and the scale given only applies to Gedemara. The actual distance between the two areas of bush is just under one and a half miles at the nearest point. The vegetation is also shown in fig. 1. The area of tall *Acacia spirocarpa* and *A. xanthophloea* in the north-west corner contains a good deal of thicket and the grass is tall and dense.

The *A. spirocarpa* parkland is much more open near ground level than the closed woodland. The *Combretum*-other species woodland is also very open near ground level and the grass is scanty and only moderately tall. The riverine vegetation is not uniform, thorn thicket and clump thicket both being present and in a few places one bank or the other is clear of bushes.

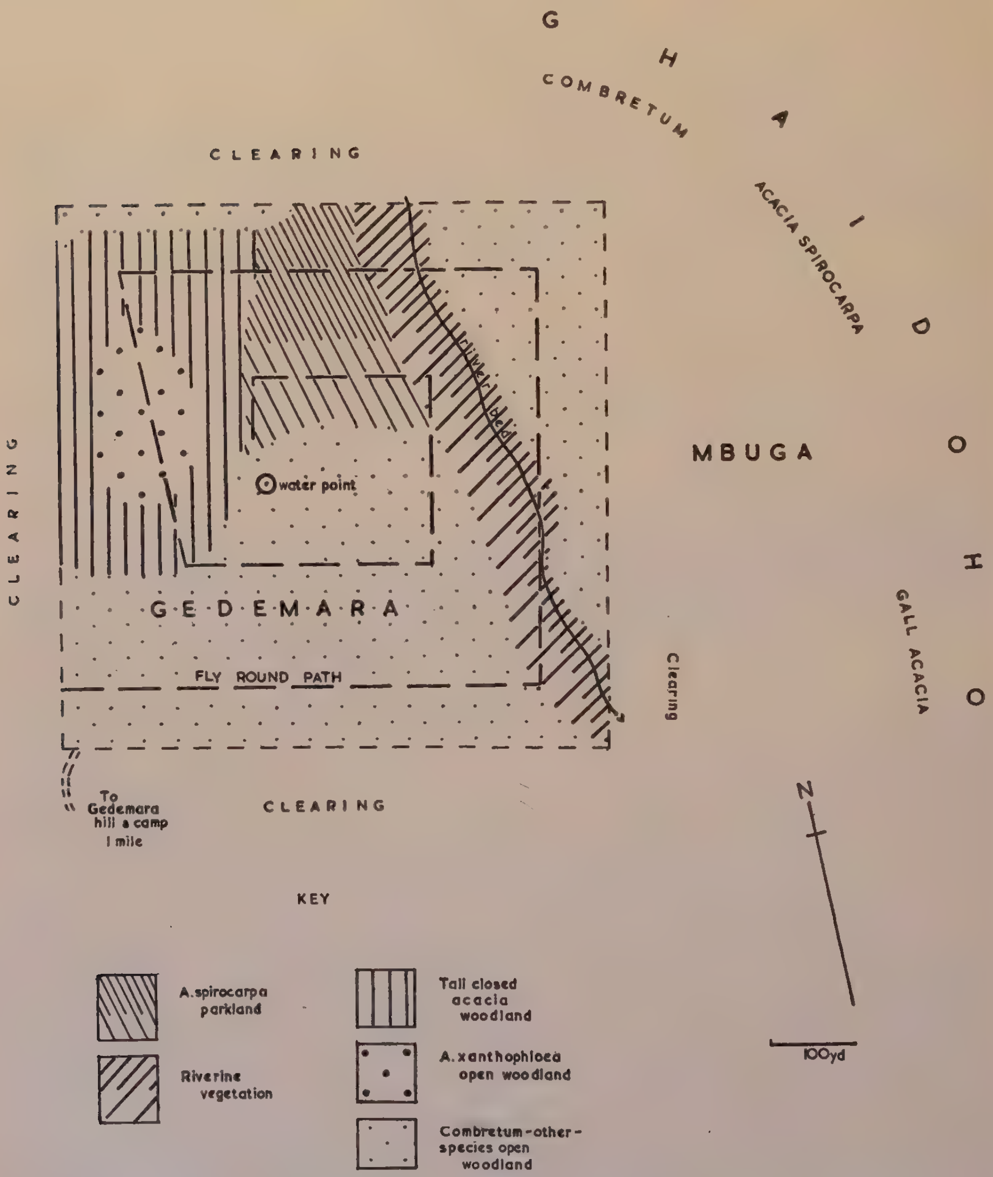

GHAIDOHO
COMBRETUM
ACACIA SPIROCARPA
MBUGA
GALL ACACIA
Clearing
CLEARING
CLEARING
CLEARING
water point
GEDEMARA
FLY ROUND PATH
To Gedemara hill & camp I mile
N
100yd
KEY
A. spirocarpa parkland
Riverine vegetation
Tall closed acacia woodland
A. xanthophloea open woodland
Combretum-other-species open woodland

Fig. 1.—Semi-diagrammatic map of experimental area to show the main vegetation zones and fly-round path in Gedemara, and the general relation of the block to Ghaidoho. (Modified from map by J. A. Gledhill.)

Distribution of tsetse.

G. morsitans was found principally in the tall acacia woodland and especially round the depression within it. *G. swynnertoni* occurred mainly along the eastern edge of the block. This distribution of the two species was similar to that found by Dr. C. H. N. Jackson early in 1951 (personal communication).

One *G. pallidipes* was captured in Gedemara in 1950.

Meteorology.

Meteorological readings could not be taken but rainfall figures for Kikore, about ten miles away, are given in Table I.

TABLE I.

Monthly rainfall at Kikore field station, in the same area as Gedemara, for the wet season 1951–52.

Month	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total
Rainy days	1	11	22	11	10	16	16	14	1	102
Rain (inches)	0·19	3·34	11·03	4·88	10·8	4·23	6·83	4·24	0·6	45·6

Insecticide.

It had been hoped to develop a special formulation which would be more persistent than the usual emulsions, but the expected ingredients did not arrive. It was therefore decided to use a stock of a commercial preparation marketed under the name "Rucide" by Taubmanns Pty. Ltd. (Australia). This is reported to contain 50 per cent. p,p′DDT and forms a good dispersion if carefully mixed according to instructions. Laboratory tests showed that this preparation, sprayed on calves at a strength of 10 per cent. p,p′DDT, gave a mean kill over 3 days of 93 per cent. of *G. palpalis fuscipes* Newst. applied for 15 seconds.

The stock of "Rucide" was exhausted before the end of the experiment. An emulsion concentrate was prepared by the chemistry section, Colonial Insecticide Research Unit, from available materials. This was an emergency preparation and could probably be improved on; in particular the proportion of wetting agent was restricted by supply difficulties. With distilled water a stable concentrate with a higher proportion of rosin was attainable, but with local water supplies stability could be achieved only by a reduction in this ingredient. The formula finally used was prepared in two parts, A and B.—

A	DDT technical	1350 ml.
	Rosin (locally purchased)	350 ml.
	Solvent (Petrochemicals 23–5)	1350 ml.
	Triethanolamine oleate	158 ml.
B	Water	1350 ml.
	Triethanolamine	25 ml.

The two parts, made up separately, were then mixed to make a concentrate.

The above amount of concentrate was diluted with water before application, to give three gallons of spray containing 10 per cent. technical DDT. In tests at the laboratory this was shown to be more effective than "Rucide" applied as a 10 per cent. suspension of p,p′isomer. The kill of *G. palpalis*, applied as before, was 100 per cent. for three days, 90 per cent on the fourth, giving an overall mortality for four days of 98 per cent.

TABLE 11.

Catches of non-teneral male tsetse.

Period	Gedemara		Ghaidoho	
	G. morsitans	*G. swynnertoni*	*G. morsitans*	*G. swynnertoni*
18–21 Oct. 1951 . .	79	13		
22–25	64	16		
26–29	57	12		
30 Oct.–2 Nov.	66	33		
3– 6	53	28		
EXPERIMENT STARTED (7th Nov. 1951)				
7–10	41	28		
11–14	20	13		
15–18	19	9·3		
19–22	10	11		
23–26	8	12		
27–30	9	9		
1– 4 Dec.	7	9·3		
5– 8	9	10		
9–12	5·3	9·3		
13–20	2·3	2·8		
21–28	2·3	2·8		
29 Dec. 1951–5 Jan. 1952 . .	1·1	1·7		
6–13	0·7	2·7		
14–21	3·4	2·3		
22–29	0·6	2·3	36	44
30 Jan.–6 Feb.		2·9		
7–14	0·3	1·7	24	22
15–22		1·1	27	21
23 Feb.–1 March	0·3	2·3	11	23
2– 9		2·0	6	15
10–17	0·3	2·7	18	29
EXPERIMENT ENDED (15th March 1952)				
18–25		4·0	20	37
26 March–2 April . .	0·3	1·7	8	26
3–10		2·9	10	26
11–18	0·6	0·6	14	23
19–26		1·7	11	15
27 April–4 May	0·6	0·7	3	9
5–12		1·1	7	11
13–20	0·0	1·7	6	13
21–28		2·3	7	15
29 May– 5 June	0·0	1·7	7	17
6–13		2·3	6	17
14–21	0·9	3·4	15	43
22 29		0·0	8	14
30 June–7 July	0·6	2·3	10	18
8–15		0·6	14	19
16–23	1·1	3·4	21	28
24–31		2·3	20	29
1 July–8 Aug.	0·6	2·9	14	25
9–16		2·9	20	25
17–24	0·6	2·7	17	32
25 Aug.–1 Sept.		3·4	22	38
2– 9	2·3	8·6	20	49
10–17	1·2	5·2	21	38
18–25	1·7	6·3	8	34
26 Sept.–3 Oct.	2·3	7·4	10	57
4–11	4·6	8·0	19	71
12–19	0·7	4·0	12	32
20–27	1·7	9·1	9	53
28 Oct.–4 Nov.	2·3	12	9	44
5–12	0·8	19	14	71

Actual catches in the experimental block (Gedemara) and along the edge of the bush (Ghaidoho) on the far side of the barrier clearing which separated the two areas.

Experimental procedure.

Treated cattle were first introduced on 7th November 1951 and withdrawn on 15th March 1952. The experiment started with 22 cattle, increased shortly afterwards to 26. For one week per month four oxen were detached for *G. pallidipes* rounds elsewhere and so the mean number in the block was 25, equalling 100 per square mile.

It was intended to divide these animals into four herds of five to seven and to keep each herd in one quarter of the block (one-sixteenth square mile). Owing to difficulty in getting herd boys this was not possible until February and most of the experiment was conducted with two herds of 11, later of 13, oxen. These were herded in the block by day for seven days a week.

It was expected that, at this density of cattle, game would tend to be driven out, but fly-boys reported an average of 6·9 head of game per day during their rounds, not including animals smaller than impala. The fly-rounds occupied no more than two hours each day and much game would not be seen, so the actual numbers present were certainly larger than this.

The cattle used were all small and fairly docile. They were kept in a pen about a mile from the block and sprayed twice a week with a single " Fortemist " hand-operated " onion sprayer ", which was eminently suitable for the work. The two nozzles were worked at once, one on each side of the animal. The animals were sprayed as they were driven out in the morning, the exit from the pen being a narrow crush in which they were confined singly while being sprayed. The whole animal except the head was sprayed until it was wet but not running. Expenditure was about 165 cc. per animal but full grown cattle would need 250–300 cc. Much of the spray remained on the walls of the crush or fell short and the actual amount of DDT received by each animal was certainly less than the 20 gm. expended. The process took about half an hour for the whole herd, and thus the bait was not kept out of the bush for any considerable period.

Sickly animals were tested for trypanosomes, but since diagnosis was often delayed they were treated with dimidium bromide as soon as the bloodslide had been taken. Several animals were found positive but none died from any cause during the experiment.

The killing power of the cattle in the block was tested regularly, by the method used for the original laboratory tests, on animals selected at random from the herd. Flies were applied on a fixed plan, all parts of the body being tested. In the early part of the experiment the kill, up to the third day after spraying, was not found to fall below 87 per cent. but later on it fell off more rapidly. The reasons for this are discussed later.

Fly-rounds.

Pre-treatment catches were begun on 25th August 1951. Rounds were made on six days a week between 18th October 1951 and 15th November 1952 by two fly-boys along the spiral path (fig. 1). The treated cattle were withdrawn on 15th March 1952. All flies captured were marked and released. Before the experiment started, population estimates were made and the number of flies caught when cattle were in the bush and when they were absent were compared by herding the animals in Gedemara on alternate days only. No differences were found for either species. Catching was continued for eight months after the experiment ended, and, from 13th February, catching and marking was carried on along the edge of the nearest piece of bush containing fly (Ghaidoho) with the purpose of detecting any immigration between the two areas. Catches for both areas are summarised in Table II. These figures represent the total number of non-teneral male tsetse actually captured in each successive four-day period with a fly-round made every day. If only three rounds were made in the period, the number is calculated proportionately (catch for three days × four-thirds). As numbers fell in Gedemara the four-day catch was averaged over two and later four periods. The average density for either area is readily obtained by multiplying these figures by 0·7. Treated cattle were in the area daily from 7th November 1951 to 15th March 1952.

Control figures.

There was no satisfactory control for Gedemara, but the effect of the experiment was so marked that this is not serious.

Initial numbers in Gedemara.

Estimates of the population of both species of tsetse were made during the period 24th October to 6th November by marking flies with paint and noting recaptures. From the data obtained the mean true populations of old males for the period were calculated by both the recapture plus interpolation and the re-recapture methods (Jackson, 1948). For *G. morsitans* the two methods give true populations of 110 and 138 respectively (mean 124) and for *G. swynnertoni* 62 and 54 (mean 58). The total number of adult flies present, including females and teneral males would be about thrice these numbers. A year previously the numbers were much higher, probably because flies persisted in the felled trees around the block (J. A. Gledhill, unpublished report). In April 1951 both species were less abundant than in the following October (before the experiment) (Jackson, 1953). Thus both species were maintaining themselves in this small block.

Jackson found that there was considerable migration of *G. swynnertoni* but not of *G. morsitans* between Gedemara and other tsetse-infested bush (Jackson, 1953).

Assessment of Results.

Calculation of time to achieve extermination.

It had been arbitrarily assumed that a reduction in numbers by 99·9 per cent. would be a safe estimate of extermination point. The total number of female *morsitans* was originally probably about twice that of the males—say 250, and a reduction to 1/1,000th would leave 0·25 females. Reduction of *G. swynnertoni* to the same absolute level would be achieved when 2/1,000th of the original numbers remain. Extermination time can be calculated (Whiteside, 1949) or obtained more simply graphically. In the present case only males are numerous enough to work with. Females come to the bait less frequently than males and will be reduced more slowly at first. However, after this initial depletion the number of males depends on the rate of reproduction, *i.e.*, the number of females present. Although females always exceed males in numbers the assumed level of extermination was made so conservative that it is likely that a reduction of males to 1/1,000th would be accompanied by extermination of the females.

To determine the extermination time graphically, catches have been plotted against time (fig. 2). The total catch of non-teneral males per four-day period has been used, averaged over two or four such periods if necessary. Four days is the mean hunger cycle of both these species (Jackson; Hocking, both quoted by Jackson, 1949) and is used because each fly will have at least one chance of contacting insecticide in this period. A logarithmic scale is used since extermination proceeds approximately logarithmically (fig. 2). The dates at which elimination will be achieved are obtained by projecting the slopes of the curves of reduction, such as lines AB, AC, DE, to cut the levels of fly catches which are assumed to be equivalent to extermination. These are taken in the present case to be 0·1 and 0·2 per cent., respectively, of the initial levels A and D for *G. morsitans* and *G. swynnertoni*. In fig. 2 the initial numbers at these points are the means for each species for the four-day period prior to introducing bait cattle, but are transposed to day 0 for the purpose of calculation.

Course of Experiment.

Reduction in the two species of tsetse.

The final percentage reduction achieved in old males of the two species was 99·5 per cent. for *G. morsitans* and 92·5 per cent. for *G. swynnertoni*. Table II gives details of the routine standard catches of non-teneral males. These are expressed as the total catch per four consecutive days (which is the mean hunger cycle). When fly became scarce, catches were averaged over two or four hunger cycles.

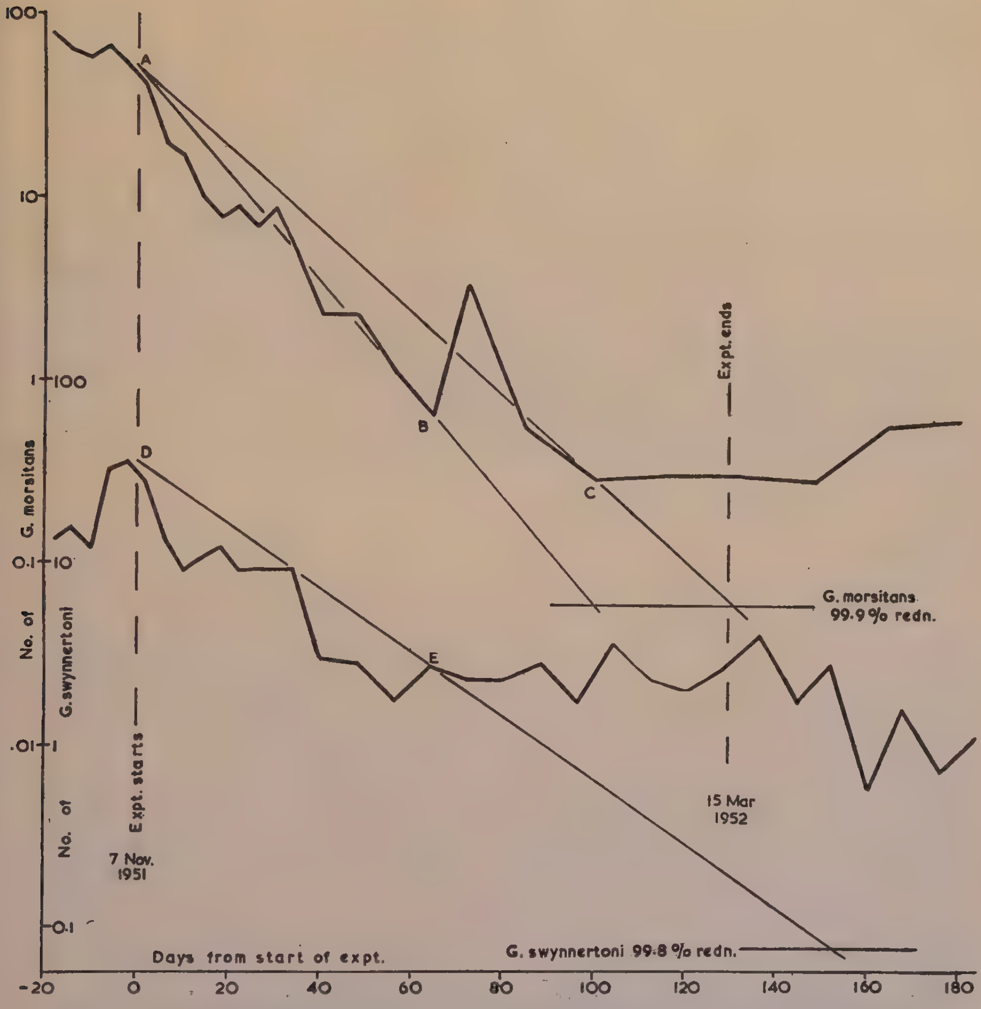


Fig. 2.—The fall in tsetse numbers (non-teneral males) in Gedemara during the experiment. The data plotted are those given in the early part of Table II.

When probable extermination times were obtained graphically after the end of the second pupal period they were found to be 100 days for *G. morsitans* and

152 days for *G. swynnertoni* (fig. 2). The end point for *G. swynnertoni* was so far distant that it was decided to work on *G. morsitans* alone. Between the 69th and 79th day of the experiment there was a sharp increase in the catches of this species. This was not maintained however, and by the hundredth day it seemed that the slope of the curve of reduction had returned to normal, although offset along the axis of time. The probable end point was now recalculated using the same original population as before, since this would give the most conservative estimate of rate of fall in numbers and the most conservative end point (fig. 2). The new end point was day 129. This was over a month after the first estimate, supplies of insecticide were exhausted by this date, and the experiment was therefore terminated on day 130, 15th March 1952. By this time it had become evident that no further reduction in numbers of *G. morsitans* had been achieved over the previous month, while *G. swynnertoni* had actually increased in numbers after remaining sensibly constant since the sixth week of the experiment.

After-effects of experiment.

In contrast to Whiteside's results on *G. pallidipes* (Whiteside, 1949) there was no sudden rise in catches immediately after the end of the experiment, both species showing their normal seasonal trend in average densities. The average density of *G. swynnertoni* fell slowly, to rise slowly again at the end of the rains. Catches of *G. morsitans* also rose slightly over the first eleven weeks and then fell to nothing for a month. In the middle of June there was a sudden increase when three flies were caught in three rounds. This increase will be discussed later, but the absence of an immediate rise is thought to be due to the continuation of the experiment for a full pupal period after stability had been achieved, thus bringing the numbers of pupae down to the number equivalent to the adult population.

Discussion.

Reasons for failure to achieve elimination.

Likely reasons for failure to achieve elimination after a promising start may be classified under three headings. The first concerns possible density-dependent factors on which there is no data. The second concerns a falling-off in the effectiveness of the cattle as bait. This certainly occurred for two reasons. The actual lethal power of the cattle diminished due to removal of insecticide from the belly, legs and lower flanks of the animals by the rubbing of the rapidly growing, frequently wet herbage. This was shown in the regular tests made on animals from the herd, their upper parts remaining lethal for four days even when their lower parts became innocuous. This loss of lethality is not thought to be due to the change to the laboratory-prepared emulsion. It is also thought that contact between fly and bait was progressively reduced because the small cattle became almost hidden by the tall grass in parts of the block. This doubtless applied also to the smaller species of game but the larger kudu, roan and hartebeest would still be conspicuous. In addition, with abundant grazing there was less movement and more lying-down than in the short-grass season. During this period too, tsetse feed only half as frequently as in the dry season and the females would therefore have only half the opportunity to make contact with the insecticide.

The third possible reason for failure is immigration from other infested areas. For many months flies were captured and marked in an effort to obtain direct evidence. Two male tsetse, which had been marked in Gedemara, were recaptured in Ghaidoho. One of these (*G. morsitans*) had been marked a month before recapture but the other (*G. swynnertoni*) had been marked the previous day and may have followed the fly-boys across. There is also indirect evidence.

Sudden increases in catches in Gedemara have on several occasions been coincident with or followed similar rises in Ghaidoho (Table II). These might be due to the common influence of the weather but the increases in catches were usually accompanied by an influx of game into the experimental block. For instance, the jump in catches of both species between 14th and 21st January coincided with the arrival of herds of impala and kudu and several hartebeest. The increased catches of 14th–21st June and 16th–23rd July were accompanied by reports of game, and during October and November animals were constantly entering the block. If immigration was taking place constantly a steady rise in the numbers of tsetse in Gedemara would be expected. However, from early April to 31st August all tsetse captured were killed and this may have been sufficient to delay the increase which eventually occurred in September and October.

Finally, Dr. C. H. N. Jackson in the previous wet season found considerable migration, between Gedemara and neighbouring bush, of *G. swynnertoni* but not of *G. morsitans* (Jackson, 1953). Taking the evidence as a whole it seems that there was a fairly steady and comparatively large immigration of *G. swynnertoni* while *G. morsitans* came in spasmodically, assisted by movement of game.

Difference in the effect on the two species.

Comparison of catches made before the experiment started with those made in its later stages, after the large initial reduction in tsetse numbers, show that in all parts of Gedemara *G. morsitans* was reduced to a greater extent than *G. swynnertoni*. This could be due to a greater partiality for cattle by the former, for which there is no evidence. It is more likely to be due to a difference in the rate of immigration, as suggested above. Even if there is no difference in the natural mobilities of the two species, *G. swynnertoni* was the more abundant in Ghaidoho and inhabited principally the thorn bush, past which a great deal of game movement took place. It would therefore cross the barrier clearing more frequently.

Conclusions.

There was an undoubted falling-off in the effectiveness of the bait cattle but it is considered that there was sufficient immigration of both species for this to have been the real reason why elimination was not achieved. Loss of effectiveness would slow down the rate of fall in numbers but immigration is more likely to be able to reverse it, as happened in the case of *G. swynnertoni*. Moreover, migration of this species would be expected to be greater and is known to have been so the previous season. It is the most likely reason for its greater persistence compared with *G. morsitans*. The occurrence of immigration makes it quite impossible to say whether these species of tsetse might be exterminated by this method if the area were completely isolated, as it is not known what will happen at extremely low densities of fly.

Possibilities of improving the method include the use of different insecticidal preparations. DDT is the insecticide of choice. BHC is too volatile for use outdoors in the tropics, toxaphene is less effective and dieldrin too toxic to cattle (unpub. obs.). If the DDT were fixed more firmly to the coat to prevent removal by vegetation it might be too firmly attached for the tsetse to pick up a lethal dose in the short period of contact. However, it may be possible to obtain a better compromise than hitherto. The most promising measures open to us are to increase the effectiveness of the bait by using larger and possibly more numerous animals when the grass is short, at the end of the dry season and beginning of the short rains, although at this time the numbers will be limited by the amount of grazing available in the bush. The advantages gained are greater visibility and mobility of the bait and greater persistence of the insecticide. In addition the shorter hunger cycle will increase the chances of females contacting the bait before they larviposit for the first time. Additional measures include removal of wild game and division of the main herd into small parties.

It is concluded that, although the possibility of complete extermination remains doubtful, the method will rapidly reduce the numbers of both *G. morsitans* and *G. swynnertoni* to very small proportions even in unfavourable conditions. As in all methods for controlling tsetse by means of insecticides proper isolation of the area from immigration is essential.

Summary.

An experiment was carried out in a small block of mixed bush in Tanganyika in an attempt to eliminate the two resident species of tsetse fly, *Glossina morsitans* Westw. and *G. swynnertoni* Aust., by means of bait cattle treated with DDT. Small cattle were used at the rate of 100 per square mile in herds of 12 or 13 per one-eighth of a square mile. Their numerical superiority over the large game was no more than about 3 : 1.

The cattle were sprayed twice weekly. Originally a 10 per cent. suspension of the p,p′isomer was prepared from a commercial formulation of DDT. Later a laboratory-prepared emulsion (10 per cent. technical DDT) was used.

Extermination was expected with a reduction in numbers of old male tsetse of 99·9 per cent. In practice *G. morsitans* was reduced by 99·5 per cent. and *G. swynnertoni* by 92·5 per cent.

It is considered that there was sufficient immigration across the barrier clearing to account for the failure to achieve extermination of either species. It is not possible to say if extermination would have been attained in the absence of immigration.

It is considered that with the insecticidal formulations now available there is not much prospect of improving on these results in similar conditions although a great reduction in tsetse numbers is possible and might stop the carrying of disease. In the dry season, after the grass has been burnt, there is better prospect of success.

Acknowledgements.

The treatment of the data obtained in this experiment is due to Mr. E. F. Whiteside, late of the East Africa Tsetse and Trypanosomiasis Research and Reclamation Organisation, to whom I am much indebted. My thanks are due to the following members of the Colonial Insecticide Research Unit: to Mr. K. S. Hocking, officer i/c, for much preliminary planning, to Messrs. R. C. Sell and S. Znatowicz, who carried out the field work, and to Dr. J. Robinson, who devised and manufactured the laboratory emulsion, for which the special solvent was provided free of charge by Petrochemicals Ltd., U.K. Dr. C. H. N. Jackson, of E.A.T.R.O., kindly assisted in the population estimate, and to him and Mr. J. A. Gledhill I am indebted for permission to quote their unpublished observations. The experiment was financed from Colonial Development and Welfare funds under direction of the Colonial Insecticides, Fungicides and Herbicides Committee.

References.

Jackson, C. H. N. (1948). The analysis of a tsetse-fly population. III.—Ann. Eugen., Lond., **14**, pp. 91–108.

Jackson, C. H. N. (1949). The biology of tsetse flies.—Biol. Rev., **24**, pp. 174–199.

Jackson, C. H. N. (1953). A mixed population of *Glossina morsitans* and *G. swynnertoni*.—J. Anim. Ecol., **22,** pp. 78–86.

Whiteside, E. F. (1949). An experiment in control of tsetse with DDT-treated oxen.—Bull. ent. Res., **40,** pp. 123–134.

THE MOSQUITOS OF AITUTAKI, SOUTHERN COOK ISLANDS.[1]

By Marshall Laird, M.Sc., Ph.D.[2]

L.G.

(Plate XXXV.)

The Cook Islands, dependencies of New Zealand, comprise two scattered groups bounded by the Latitudes of 8° and 23°S. and the Longitudes of 156° and 167°W. Aitutaki belongs to the Southern or Lower Cook Islands, and lies in Lat. 18°55′S., Long. 159°45′W. It is an atoll, the main island of which is of partly volcanic formation. Non-periodic filariasis occurs there, data gathered by Lambert (1926) indicating a microfilaria rate of approximately 50 per cent., while Davis (1949) found microfilariae in the blood of 102 of 240 subjects over nine years of age.

Only one species of mosquito, *Aëdes* (*Stegomyia*) *polynesiensis* Marks (1951*b*) (= *A. pseudoscutellaris* (Theobald) in part) has previously been recorded from Aitutaki. This insect is the intermediate host for *Wuchereria bancrofti* in the Cook Islands (McKenzie, 1925; Davis, 1949).

Lambert (1926) worked in the southern part of the group from November 1925 until January 1926, and sent the mosquitos which he collected to Dr. F. M. Root at Johns Hopkins University. He found "*Stegomyia pseudoscutellaris*" to be especially prevalent, and thought that he "recognized most of the familiar forms of Fiji and Tonga" (Lambert, 1926). According to a letter from Dr. Root to Dr. Buxton (Buxton & Hopkins, 1927), however, Lambert collected only "*Aëdes variegatus* var. *pseudoscutellaris*" at Aitutaki, while at Rarotonga he found this species and but two others, *Aëdes* (*Stegomyia*) *argenteus* (Poiret) (= *A. aegypti* (L.)) and *Culex* (*Culex*) *fatigans* Wiedemann (= *C. pipiens fatigans* Wied.). Buxton & Hopkins thought it probable that an undetermined *Aëdes* which McKenzie (1925) collected at Rarotonga was *Aëdes* (*Aedimorphus*) *vexans* (Meigen); but no records of this species from the Cook Islands have since been published. Finally, Davis (1949) mentioned the occurrence of *Culex* (*Culex*) *annulirostris* Skuse in Rarotonga.

Marks' (1951*a*) synopsis of the mosquitos known from south-eastern Polynesia contains no information additional to that given above concerning the Culicidae of the Southern Cook Islands, and fails to note Davis' record of *C. annulirostris* from Rarotonga. The only other relevant data which I have been able to discover, concern the introduction of *Gambusia* into the Lower Group Islands (Anon., 1936, 1937).

Our knowledge of the mosquitos of the Cook Islands thus being virtually confined to Rarotonga, advantage was taken of a routine flight by an RNZAF aircraft to undertake a brief mosquito survey at Aitutaki. Collections were made throughout the main island of this atoll from 14th to 16th March 1953.

Results of the Survey.

A total of seventeen mosquito larval habitats of all kinds were investigated, with the results summarised in Table I.

---

[1] These studies form part of a project initiated by the Royal New Zealand Air Force and supported by a grant from the N.Z. Department of Scientific and Industrial Research. Their publication is authorised by the Chief of Air Staff, RNZAF.

[2] Medical Branch, RNZAF.

TABLE I.

Synopsis of larval records.

Species	Habitats	No. of times collected
Aëdes polynesiensis	Petrol drums (3), coconut husk (1), rot-hole in tree (1), beached canoe (1), whaling try pot (1), truck tyre (1)	8
Culex pipiens fatigans	Steel tank containing water with masses of decomposing vegetation and other organic débris (1), beached canoe (1), petrol drum (1)	3
Culex annulirostris	Irrigation ditches between taro beds (5), borrow pits (2), swamp (1), beached canoe (1)	9

The following larval associations were noticed :—

A. polynesiensis, *C. pipiens fatigans* and *C. annulirostris* (once, in beached canoe);

A. polynesiensis and *C. pipiens fatigans* (once, in petrol drum).

A. polynesiensis was by far the most troublesome mosquito throughout Aitutaki at the time of my visit. Adults were collected while attempting to bite during the hours of daylight, both in areas of dense vegetation and inside houses at the villages. *C. annulirostris* was quite common at night from end to end of the island; while adult *C. pipiens fatigans* were never seen at all.

All five of the irrigation ditches in which *C. annulirostris* larvae were found supported various other aquatic insects. Species of significance as mosquito predators included the larval stages of the dragonflies *Pantala flavescens* (F.) and *Diplacodes bipunctata* (Brauer) and those of the damselfly *Ischnura a. aurora* (Brauer). These insects have all been recorded from Rarotonga (Lieftinck, 1953). The only Hemiptera collected were water-striders, surface-feeders which are known to attack mosquitos on occasion (Hinman, 1934); two species were noticed, *Microvelia* sp. *oceanica* group, and a Gerrid, *Limnogonus* sp. or *Gerris* sp.

Two of the ditches supported *Gambusia* while the other three did not, although all five were otherwise closely comparable both physically and biologically. In those having top minnows, mosquito larvae were rare, being dipped only from the shelter of thick marginal clumps of emergent grasses. By contrast, up to 400 larvae per square foot of water surface were counted in the open parts of the ditches lacking these fishes. The value of *Gambusia* in controlling *C. annulirostris* at the atoll is thus self-evident. Top minnows were not, however, found in the breeding places of either of the other species of mosquitos. The larval habitats of *A. polynesiensis* and *C. pipiens fatigans* were, in fact, quite free from predators of any kind.

Discussion.

A much longer survey would have to be undertaken at Aitutaki before the non-occurrence of *Aëdes aegypti* and *A. vexans* could be taken as established. An abundance of larval habitats suited to the requirements of both these species is certainly available there. Such " domestic " breeding places of *A. polynesiensis* as the 44-gallon drum illustrated in Plate XXXV, fig. 1, could undoubtedly harbour the aquatic stages of *A. aegypti*; while, in the South Pacific, populations of *C. annulirostris* and *A. vexans* often alternate with one another in the more temporary kinds of ground pools, explosive appearances of the latter species being correlated with season and rainfall (Buxton & Hopkins, 1927).

Davis (1949) thought it fairly certain that *A. polynesiensis* had reached the

Cook Islands before the arrival of Europeans, and suggested that the original introduction may have followed the carriage of larvae in the drinking-water containers used in the old Polynesian ocean-going canoes. It was of interest in this connection to find all three species of mosquito now known from Aitutaki represented in the larval collection from a beached canoe at Tekoutu (Pl. XXXV, fig. 2). The photograph shows how the islanders keep palm leaves over canoes not in use, the intention being to keep water out. In practice a certain amount of water always seeps through. Shade being provided by the leaves, the resulting infusion becomes an excellent larval habitat for certain mosquitos. Although the baling-out of the canoes before use removes many of the eggs, larvae and pupae, others remain. Adults may likewise stay aboard in the shelter of the bow- and stern-covers. Provided that the mosquitos concerned can withstand the effects of salt spray and of increased salinity in the bilge, the introduction potential is obvious. Buxton & Hopkins (1927), who demonstrated that the eggs of Samoan "*A. variegatus*" (= *A. polynesiensis*) are resistant to drying, were of the opinion that "the distribution of this mosquito . . . has been partly effected in canoes."

As regards the recording of *Culex pipiens fatigans*, Buxton & Hopkins brought forward evidence indicating that this species is a comparative newcomer to the South Pacific. A "domestic" mosquito well suited to survive and breed on board ships, *C. pipiens fatigans*, although apparently absent from Aitutaki at the time of Lambert's visit just over a quarter of a century ago, would not have lacked the means of reaching that island from Rarotonga.

Although there was no definite record of *C. annulirostris* from any of the islands east of Samoa when Buxton & Hopkins published the results of their researches, it is probable that the species was in fact then established among these islands. In 1934, E. C. Zimmerman of the Bernice P. Bishop Museum's Mangarevan Expedition collected *C. annulirostris* at Tahiti and Raiatea (Society Is.), Fakarava (Tuamotu Is.) and Rimatara (Austral I.) (Marks, 1951*a*). It is unlikely that the insect would have attained as wide a distribution as this in so short a period. Be that as it may, in view of the occurrence of this species in all suitable larval habitats at Aitutaki, and the fact that in the tropical Pacific in general, *e.g.*, Samoa (Buxton & Hopkins, 1927), its larvae are to be found throughout the year, it is unlikely that Lambert would have overlooked it had it been present in the Southern Cook Islands by 1925–26.

It was stated in the Report of the Cook Islands Administration for 1935–36 (Anon., 1936) that *Gambusia* "were introduced into Rarotonga over eighteen months ago, and have been liberated in many places in Rarotonga and also in the Lower Group Islands. They have multiplied rapidly, and are assisting in bringing the mosquito pest under control." A year later (Anon., 1937) it was claimed that "the gambusia, or mosquito-eating fish, is multiplying rapidly throughout the Lower Group and is effective in reducing the mosquito pest, and will assist in preventing the spread of filariasis."

Now the three mosquitos known from the Group at the time of Lambert's visit (*A. aegypti*, *A. polynesiensis* and *C. pipiens fatigans*) utilise small collections of water in natural or artificial containers as larval habitats. Such places are quite unsuited to *Gambusia*, which flourishes in surface waters of various types. *A. polynesiensis* being the most significant (McKenzie, 1925) if not the only (Davis, 1949) vector of *Wuchereria* in the Cook Islands, it is hard to see how the introduction of *Gambusia* could have been expected to assist in preventing the transmission of filariasis in the Group. Unless *Aëdes vexans* is in fact established in these islands—and in view of the entire absence of records of this species since the doubtful one in 1925, it is practically certain that this is not the case—the reduction of the mosquito pest claimed in 1936–37 is not referable to any species other than *C. annulirostris*.

It thus seems likely that *C. annulirostris* became established in the Southern Cook Islands during the decade 1925–1935. Like *C. pipiens fatigans*, this mosquito lends itself to accidental distribution through human agency. In 1929, for example, larvae were discovered in the hold of a ship which had arrived at Auckland, New Zealand, from Suva, Fiji (Graham, 1939). More recently, *C. annulirostris* adults, including a living female, have been collected on board aircraft following their arrival at Whenuapai Airport, Auckland, from Australia, Norfolk Island and Fiji (Laird, 1951). Pratique for the Group being granted at Rarotonga, one would imagine that that island would have been the first to be invaded. The introduction, by an inter-island vessel, might have been made either from Samoa or some other place to eastward or, at least in the latter stages of the decade in question, from the Society Islands.

C. annulirostris once having become established at Rarotonga, small vessels trading within the Cook Group could easily have distributed the species among the other islands. It is probably to be found at Mauke Island as well as at Aitutaki, for there is a statement from the Resident Agent at the former place that "the mosquito-eating fish (gambusia) introduced here last year have been liberated in all the fresh-water swamps on the Island and have increased by millions, and have greatly reduced the mosquito pest" (Anon., 1936).

Summary.

Aëdes (*Stegomyia*) *polynesiensis* Marks, *Culex* (*Culex*) *pipiens fatigans* Wiedemann and *Culex annulirostris* Skuse were collected at Aitutaki, Southern Cook Islands, during a brief visit in 1953. Possible means of introduction of these mosquitos are discussed.

Acknowledgements.

The Resident Agent extended every courtesy, while transport and other assistance were provided by the representative of the N.Z. Civil Aviation Branch. The local Cook Islands Medical Practitioner, Teariki Matenga, helped with much of the collecting. I am indebted to Dr. M. A. Lieftinck, of Bogor, Indonesia, for identifying the Odonata, and to the Commonwealth Institute of Entomology for handling the Hemiptera.

References.

Anon. (1936). Report of Cook Islands Administration, 1935–36.—N.Z. Parliam. Pap., no. 1-A.3., pp. 1–31.

Anon. (1937). Report . . . 1936–37.—*Ibid.*, no. 1-A.3., pp. 1–28.

Buxton, P. A. & Hopkins, G. H. E. (1927). Researches in Polynesia and Melanesia. Pts. I–IV.—Mem. Lond. Sch. Hyg. trop. Med., no. 1, 260 pp.

Davis, T. R. A. (1949). Filariasis control in the Cook Islands.—N.Z. med. J., **48,** pp. 362–370.

Graham, D.H. (1939). Mosquito life in the Auckland District.—Trans. roy. Soc. N.Z., **69,** pp. 210–224.

Hinman, E. H. (1934). Predators of the Culicidae (Mosquitoes). I. The predators of larvae and pupae, exclusive of fish.—J. trop. Med. Hyg., **37,** pp. 129–134.

Laird, M. (1951). Insects collected from aircraft arriving in New Zealand from abroad.—Zool. Pub. Vict. Univ. N.Z., no. 11, 30 pp.

LAMBERT, S. M. (1926). Health survey of the Cook Islands, with special reference to hookworm disease. Appendix to Report of Cook Islands Administration.—N.Z. Parliam. Pap., no. 1-A.3., pp. 27–40.

LIEFTINCK, M. A. (1953). Notes on some dragonflies (Odonata) of the Cook Islands.—Proc. Hawaii ent. Soc., **15**, pp. 45–49.

McKENZIE, A. (1925). Observations on filariasis, yaws and intestinal helminthic infections in the Cook Islands with notes on the breeding habits of *Stegomyia pseudoscutellaris*.—Trans. R. Soc. trop. Med. Hyg., **19**, pp. 138–149.

MARKS, E. N. (1951*a*). Mosquitoes from southeastern Polynesia.—Occ. Pap. Bishop Mus., **20**, pp. 123–130.

MARKS, E. N. (1951*b*). The vector of filariasis in Polynesia: a change in nomenclature.—Ann. trop. Med. Parasit., **45**, pp. 137–140.

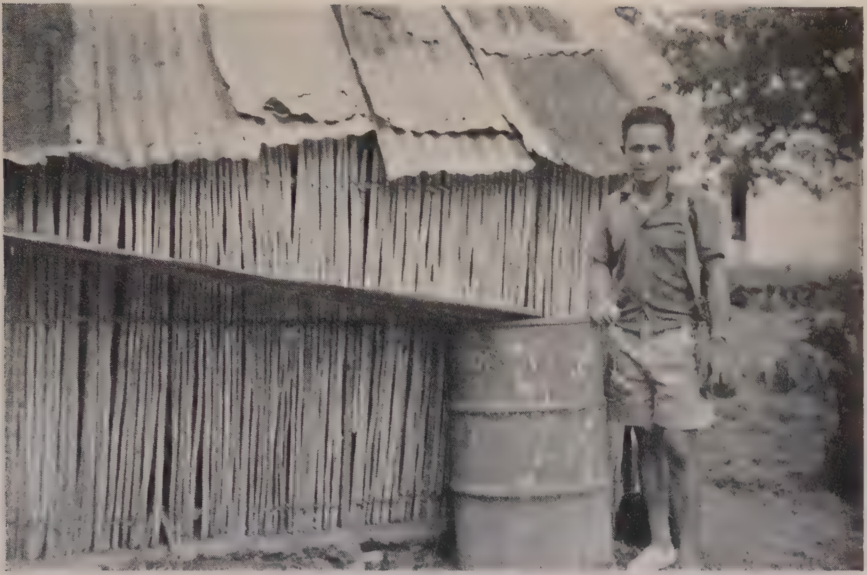


FIG. 1. Illustrating a method of obtaining rain-water commonly employed at Aitutaki. The corrugated iron sheet down which the water runs into the drum, provides a considerable degree of shade at the water surface. Water in the drum figured held many larvæ of *Aëdes* (*Stegomyia*) *polynesiensis* Marks, and appeared suited to the needs of *A. ægypti*.

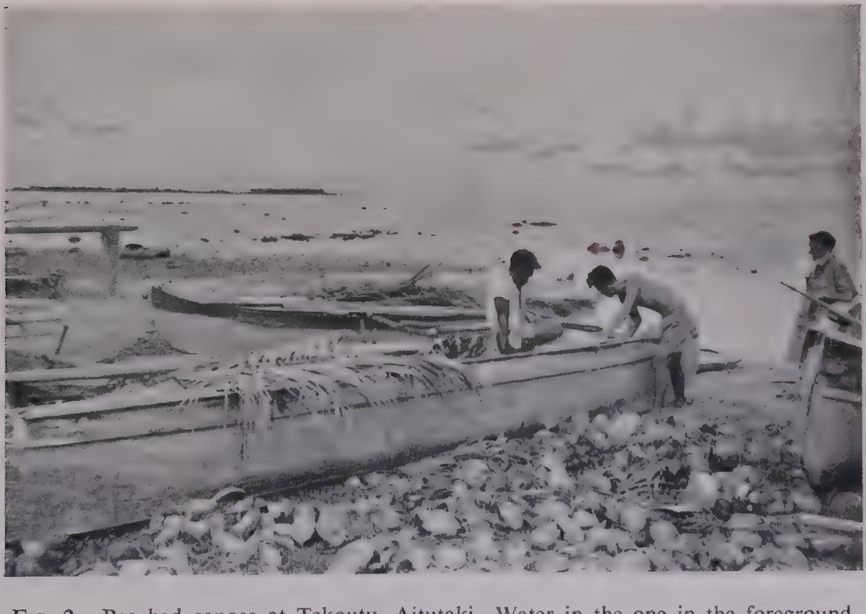


FIG. 2. Beached canoes at Tekoutu, Aitutaki. Water in the one in the foreground contained larvæ of all three species of mosquito now known from the Island. Note the longitudinally arranged coconut palm leaves which, by heavily shading the water surface, help to make the larval habitat an ideal one for such species as *A. polynesiensis*.

SOME NOTES ON THE LIFE-HISTORY AND HABITS OF *THERAPTUS* SP. (COREIDAE).*

By E. M. Tait, B.Sc.

Coconut Pest Research, Agriculture Dept., Zanzibar.

A Coreid bug of the genus *Theraptus* was observed by Way (1951) to be one of the main causes of the fall of immature coconuts in Zanzibar. Both adults and nymphs feed on young nuts which, as a result of the damage caused, later develop necrotic lesions. Nuts so damaged usually fall from the palms and where infestation is heavy very few nuts develop to maturity.

Life-History in the Laboratory.

Various instars of *Theraptus* were collected from coconut palms in the field and reared individually in wire-gauze cages in a covered outdoor insectary. Fresh undamaged spadices one to three months old were provided as food and changed about every three days. The spadices were placed in a jar of water, the mouth of which was covered with muslin to prevent the insects falling in.

Temperatures were registered by a thermograph placed in the insectary. The duration of the different stadia, the length of life of the adults, and the number of eggs laid per female were recorded individually. Batches of insects were reared in this way during the cool season from June to September 1951, and also in the hot season from November 1951 to March 1952.

It was observed that the length of the different instars varied according to temperature and, to a certain extent, to the type of food available. Insects fed on beans (*Vigna* sp.) were of a healthier appearance than those reared on coconuts, and the length of time between each moult was shorter. A diminution in the time interval between moults was also observed during the hot season when the whole development cycle was quicker and the adults lived for a shorter period.

A fertilised female usually started ovipositing about eight days after emergence and carried on laying until death one to two months later. The highest numbers of eggs recorded for single females were 126, 144 and 167. It was observed on occasion that virgin females will lay infertile eggs, but on being introduced to a male subsequent eggs were fertile. The adult life of the male is longer than that of the female, the longest lives recorded being 84, 83 and 84 days for males and 49, 66 and 73 days for females. The age of the insects did not appear to affect fecundity. Copulation takes place several times during the adult life, coitus lasting two to three hours. The females were rarely found to oviposit on the spadices, most of the eggs being laid singly on the sides of the cages, two to nine eggs being laid per day.

Eggs take from six to nine days to hatch, depending on temperature and humidity. An experiment was conducted to find out the rate of development of the egg at different temperatures. Batches of ten eggs each were placed in incubators set at different temperatures, ranging from 23·9° to 34°C., the humidity being kept high. It was observed that eggs at 23·9°C. took an average

---

[*] This species, which has hitherto been referred to in the literature as *Theraptus* sp., is now known not only to be a new species but to belong to a new genus, the descriptions of which are shortly to be published by Mr. E. S. Brown. In the present paper it will continue to be referred to as *Theraptus* sp. Ed.

TABLE I.

Length of life-cycle under different conditions.

	Average temperature 24°C. Insects fed on coconuts Time in days				Average temperature 28°C. Insects fed on coconuts Time in days				Average temperature 28°C. Insects fed on beans (*Vigna* sp.) Time in days			
	Min.	Max.	Mean	No. of individuals	Min.	Max.	Mean	No. of individuals	Min.	Max.	Mean	No. of individuals
Egg stage	8	9	8	6	6	7	6	5	6	7	6½	13
1st nymphal stage	3	4	3	21	2½	3	3	20	2	3	2½	22
2nd ,, ,, ...	5	10	7	20	2	11	5	12	4	7	4½	21
3rd ,, ,, ...	7	7	7	14	2	6	4	5	2	5	3	18
4th ,, ,, ...	5	8	6	12	3	7	4½	5	3	4	3½	14
5th ,, ,, ...	8	9	8½	11	8	9	8½	2	5	8	6	12
Mean total duration of egg and nymphal stages			39½				31				26	

of nine days to develop and at higher temperatures, from 29° to 34°C., an average of six days, but at temperatures over 33°C. the nymphs emerged from the eggs in a poor condition.

Life-History on Coconut in the Field.

Nymphs and adults of *Theraptus* have been found in the field on coconut spadices. Eggs are rarely found; one or two only have been found on the spadix at the base of the female coconut flowers, but on no other part of the palm crown although careful searches have been made. First-instar nymphs have never been found, possibly due to the fact that this stage only lasts two to three days. In the laboratory the mortality rate during the first instar is high, but it decreases with age and by the time the third instar has been attained the insect is no longer delicate. Later instars are found frequently on the young spadices but less frequently on the older ones. They have never been observed on any other parts of the palm. Adults are not often seen, probably because they are disturbed and fly away while the observer is climbing the palm.

Other Food Plants.

Theraptus has been found in the field feeding on fruits of cacao, mango, guava and cinnamon, but in all cases only immature fruits were being attacked. Although the bug has been successfully reared in the laboratory on beans (*Vigna* sp.) a prolonged and careful search in the field indicates that legumes are not normal host-plants.

Attempts were made to rear *Theraptus* on a variety of wild fruits, particularly leguminous pods (other than *Vigna*) and figs, as well as on cultivated fruits such as papaw, pineapple and citrus, but without success.

It would appear that the coconut palm is the primary host-plant and that guava and mango are only attacked during their fruiting seasons. The attacks observed on cacao and cinnamon may perhaps be regarded as departures from the normal as neither of these crops is widely cultivated in Zanzibar.

Enemies of *Theraptus*.

The most important enemy of *Theraptus* is the predacious tree-nesting ant *Oecophylla longinoda* (Latr.). Where this species is found nesting in the palms or even foraging in sufficient numbers, *Theraptus* is absent and, consequently, there is little or no damage to the developing nuts.

One Reduviid, not yet identified, has been found to feed on *Theraptus* in the field and several species will do so in the laboratory, but it seems doubtful whether these could be used for biological control.

A Strepsipteran parasite, unidentified, was discovered on *Theraptus* adults in an isolated area of guavas. Several of these parasitised adults were brought into the laboratory and put in cages with unparasitised adults and nymphs, but in no instance did any of the other insects become parasitised. No male parasites were observed. In all cases the parasitised *Theraptus* adults were sterile.

Two unidentified species of Hymenopterous egg-parasites were discovered in *Theraptus* eggs laid on mango fruit. In both cases the parasites took a further two to three weeks after collection to emerge.

It would appear that certain small ants, particularly *Pheidole megacephala* (F.), play a part in the control of *Theraptus* by carrying away the eggs. Batches of about thirty fertile eggs were placed on mango fruit at various times and in each case only about 50 per cent. hatched out, the rest being either carried away or eaten *in situ*.

Damage to Coconuts by *Theraptus*.

Experiments were carried out in the field to discover details of *Theraptus* damage on coconuts. Palms were chosen which were foraged by the ant, *O.*

longinoda, to ensure that the nuts would be free of initial *Theraptus* damage. Two second-instar nymphs were placed on each of several spadices which ranged from one which had just emerged from the spathe to one bearing mature nuts. The spadices were each enclosed in a nylon bag which was securely tied around the base to prevent ants getting in. These were examined every week, and from the results it was concluded that:—

(a) spadices bearing nuts up to three months old may be completely destroyed by one insect (nymph or adult) over a period of one month;
(b) a nut between four and six months of age, if exposed to an insect for its life-time, may be so damaged that it will fall off. If, however, it remains on the palm until it is mature it is likely to weigh less than half as much as a normal undamaged nut;
(c) nuts over six months old will not be appreciably affected by the pest;
(d) all stages of *Theraptus* will feed and develop on nuts of all ages from those on newly opened spadices to mature nuts ready for harvesting.

Damage to Cacao, Guava and Mango.

The damage on these fruits is very similar to that on the coconut. When nymphs and adults feed on the young fruit, necrotic lesions develop around the feeding site and the fruit may eventually drop off. Due to the damage caused by this pest, many mango and guava trees growing in infested coconut plantations produce no mature fruit. The necrotic areas which develop in cacao pods often become infested with moulds.

Summary.

The life-history and bionomics of the Coreid bug, *Theraptus* sp.,* which causes premature nutfall of coconuts in Zanzibar, were studied in the laboratory and in the field.

From the various experiments carried out it is concluded that:—

The development of the insect from the egg to the adult took from 26–39½ days depending on temperature and the food available.

The average length of life of the female is 45 days during which time she may produce over 100 fertile eggs.

The primary host-plant of *Theraptus* is the coconut palm, but the bug readily infests mango, guava, cinnamon and cacao trees when they are fruiting.

The pest will attack and develop successfully on nuts from the newly emerged to the mature ones.

Agents which exert a measure of biological control include the tree-nesting ant, *Oecophylla longinoda* (Latr.), an internal Strepsipteran parasite, an unidentified Reduviid, two unidentified Hymenopterous egg-parasites and possibly some small ant species which prey on the eggs. Of these, only the ant, *O. longinoda*, is capable of giving complete protection to the palm which it occupies.

Acknowledgements.

I wish to thank Dr. F. L. Vanderplank for his kind help and criticism, the Director of Agriculture, Zanzibar, for permission to publish this paper and for the use of Government coconut plantations, and Dr. W. J. Hall, Director of the Commonwealth Institute of Entomology, for the identification of insects.

Reference.

Way, M. J. (1951). An insect pest of coconuts and its relationship to certain ant species.—Nature, Lond., **168**, p. 302.

---

* See footnote on p. 429.

SOME EXPERIMENTS IN CROSS-BREEDING OF THE COREID BUG, *THERAPTUS* SP.*

By E. M. Tait, B.Sc.

Coconut Pest Research, Agriculture Dept., Zanzibar.

Way (1951) showed that premature " nutfall " and the associated condition termed " gummosis " of coconuts in East Africa is due primarily to the developing nuts being sucked by a Coreid bug of the genus *Theraptus*. A similar type of nutfall, causing losses in coconut plantations in the South Pacific, has been proved by Phillips (1940) and O'Connor (1950) to be due to another Coreid bug, *Amblypelta cocophaga* China.

Although the damage to coconut plantations in Zanzibar and Pemba islands and along the coast of the mainland territories was similar, it had been suggested by the Director of the Commonwealth Institute of Entomology that the bugs occurring in the three areas might be specifically distinct. To test this hypothesis, and at the same time to investigate the possibilities of eliminating the bug by hybridisation on the lines suggested by Vanderplank (1947) for the elimination of *Glossina* spp., cross-breeding experiments using material from the three localities were undertaken.

Material.

Nymphs were collected from coconut palms in Zanzibar, Pemba and the Tanga area in Tanganyika Territory, and these were reared to maturity in the laboratory on young coconut spadices. The mature adults thus obtained were used for the experimental cross-breeding.

Experiments.

Assuming, for the sake of clarity, that the insects from the three different localities are in fact three separate species and using males and females from each locality, breeding could be attempted by making nine possible combinations, three of which would be intra-specific and six inter-specific. Data recorded from experiments so arranged are given in Tables I and II.

TABLE I.

Intra-specific matings. Controls.

Males		Females	No. pairs used	Females laying eggs	No. of eggs	No. of eggs hatching	% hatching
Zanzibar	×	Zanzibar	8	8	591	578	94·5
Pemba	×	Pemba	—	—	—	—	—
Tanga	×	Tanga	1	1	101	101	100

---

[*] This species, which has hitherto been referred to in the literature as *Theraptus* sp., is now known not only to be a new species but to belong to a new genus, the descriptions of which are shortly to be published by Mr. E. S. Brown. In the present paper it will continue to be referred to as *Theraptus* sp. Ed.

Intra-specific matings.

Unfortunately the results of the Pemba matings were lost and, owing to the difficulty of getting fresh material, this was not repeated. The same difficulty accounts for the fact that only one pair was recorded for the Tanga mating.

TABLE II.

Inter-specific matings.

Males		Females	No. pairs used	Females laying eggs	No. of eggs	No. of eggs hatching	% hatching
Zanzibar	×	Pemba	7	6	421	374	88·8
Zanzibar	×	Tanga	5	3	61	43	70·5
Pemba	×	Zanzibar	3	3	132	132	100
Pemba	×	Tanga	1	1	94	94	100
Tanga	×	Zanzibar	1	1	33	33	100
Tanga	×	Pemba	—	—	—	—	—

Inter-specific matings.

In these crosses at least 70 per cent. of the eggs hatched out, and in three cases 100 per cent. did so. In the Zanzibar × Tanga cross, only three of the five females produced eggs. One of these started producing eggs two days after being introduced to the male which was only one day old at the time. This female laid nineteen eggs, one of which was fertile. This strongly suggests that most of the eggs were laid before insemination took place, especially in view of the fact that the other two females produced 100 per cent. fertile eggs.

TABLE III.

Inter-specific matings, F_1 generation.

Males		Females	No. pairs used	Females laying eggs	No. of eggs	No. of eggs hatching	% hatching
(ZT)	×	(ZT)	1	1	18	6	33·3
(PZ)	×	(PZ)	2	2	19	13	68·4
(ZP)	×	(ZP)	9	8	144	86	59·7

Inter-specific F_1 *generation.*

Three F_1 generation crosses were made and the results show a much lower percentage of eggs hatching out. It should be noted that, in the (ZP) × (ZP) crosses, the first three females producing eggs did so in February when the temperature was high, being over 28°C. All these eggs failed to hatch out. Most of the eggs laid by the other females some months later, in May and June when the temperature was about 24°C., were fertile. Normally a temperature of 28°C. does not have an effect on the development of the egg, but in this particular case it may have done so.

Discussion.

The primary consideration was to determine, if possible, whether specimens of *Theraptus* collected from Zanzibar, Pemba and the mainland were specifically distinct. The cross-breeding experiments here described proved that *Theraptus* from the three localities will in fact inter-breed readily and that in the first generation a high percentage of fertile eggs results from the various crosses. In the second generation fewer eggs are produced, and the percentage fertility is much lower.

The comparatively high percentage of infertile eggs produced in the F_1 generation may of course have been due to such factors as excessive temperature, unsuitable relative humidity, careless handling of the eggs, failure to mate or partial sterility in the males. Without further trials, however, the figures obtained must be considered with reserve. The results do suggest however, that the specimens used are in fact of one species and that in the three different localities any differences are due to varietal strains.

Summary.

Theraptus sp.* from Zanzibar, Pemba and Tanganyika have been inter-bred.

Individuals of the F_1 generation are fertile, but a partial sterility in some crosses may exist.

It is concluded that there is only one species but possibly three varietal strains.

Acknowledgements.

I wish to thank Dr. F. L. Vanderplank for his kind help with the experiments and criticism of this paper and the Director of Agriculture, Zanzibar, for permission to publish.

References.

O'Connor, B. A. (1950). Premature nutfall of coconuts in the British Solomon Islands Protectorate.—Agric. J. Fiji, **21,** pp. 21–42.

Phillips, J. S. (1940). Immature nutfall of coconuts in the Solomon Islands.—Bull. ent. Res., **31,** pp. 295–316.

Vanderplank, F. L. (1947). Experiments in the hybridisation of tsetse-flies (*Glossina*, Diptera) and the possibility of a new method of Control.—Trans. R. ent. Soc. Lond., **98,** pp. 1–18.

Way, M. J. (1951). An insect pest of coconuts and its relationship to certain ant species.—Nature, Lond., **168,** p. 302.

---

* See footnote on p. 433.

2

THE CULICIDAE OF SARDINIA AND CORSICA (DIPTERA).*

By Thomas H. G. Aitken.

The literature dealing with the Culicidae of Sardinia and Corsica refers largely to Anopheline mosquitoes which were studied in the course of various malaria surveys and control projects. Scattered papers dealing with other members of the family, however, have been published occasionally.

One of the first papers on the subject concerns Ficalbi's description in 1889 of *Culex phytophagus*, which was tentatively considered to be the non-blood-sucking form of *Culex pipiens* L. so abundantly found in southern Europe. Ficalbi was professor of zoology at the University of Sassari (Sardinia) at the time, and the island was mentioned as one of the places where this species occurred. Ficalbi (1899) subsequently reduced *phytophagus* to the synonymy of *pipiens*; nevertheless he was correct in his original observation concerning the existence of two species, one of which was primarily a blood-sucker and the other a non-blood-sucker. These two species are now known respectively as *Culex molestus* Forskål 1775 and *C. pipiens* (see Mattingly & others, 1951). Several other papers referring to species occurring in these islands were published by Ficalbi (1890, 1896, 1899), one of which listed 12 of the 23 then known Italian mosquitoes as present in Sardinia. In 1900, Laveran reported the presence of *Anopheles claviger* (*maculipennis* Mg.) from the vicinity of Bonifacio, Corsica. In more recent times, Brumpt (1925), Galliard (1927*a*, 1928) and Edwards (1928) have, respectively, published lists regarding Corsican Anophelines, Culicines and the Culicidae in general.

In the course of a war-time assignment in Corsica (February–October 1944) followed by a period of residence in Sardinia (1946–1952), the writer had an opportunity to make numerous Culicid collections in both islands. Inasmuch as little was known about the Sardinian fauna, aside from the early works of Ficalbi and some more recent papers on Anophelines by Missiroli and others, it seemed opportune to consolidate the information available for the two islands and publish a more up-to-date account of the Culicidae. In doing this, I originally thought of considering only the true mosquitoes (subfamily Culicinae) and the Chaoborid gnats (subfamily Chaoborinae). Subsequently I decided to complete the family group by including a list of Corsican *Dixa* midges (subfamily Dixinae) compiled by Edwards (1928); however, in this last instance, nothing new is contributed to the literature as I made no *Dixa* collections and one can merely speculate that the same species occur in both islands.

The Sardinian material was obtained during the course of the ERLAAS Anopheline eradication project (Ente Regionale per la Lotta Anti-Anofelica in Sardegna). A full account of this project is being published (Logan & others, 1953); in it is contained a more detailed account of the Anophelines than is possible here. The ERLAAS project provided a unique opportunity to survey the mosquito fauna, as thousands of scouts were employed to look for Anophelines. Thousands of Culicines were collected at the same time, but unfortunately time and trained personnel were not available to classify them, so that the great bulk of the non-Anopheline collections were thrown out. Some, however, were saved and these have constituted an important basis for the present work.

---

* The studies upon which this report is based were initiated by the author while still a member of the armed forces of the U.S.A. and were continued under the auspices of ERLAAS, a temporary agency set up by the High Commission for Hygiene and Public Health of the Italian Government in co-operation with the Division of Medicine and Public Health of The Rockefeller Foundation.

Many species previously unknown to the islands have been uncovered, at least 20 in the case of Sardinia and three in Corsica. The total number of species (52) by genera occurring in the two islands, together with new faunal records, is summarized in the following Table. In this list several species are not included which might well be present; these are *Anopheles maculipennis* Mg. *s.str.*, *A. labranchiae atroparvus* van Thiel, *A. messeae* Flni. and *Taeniorhynchus richiardii* (Fic.) in Sardinia and *A. labranchiae atroparvus* and *Culiseta subochrea* (Edw.) in Corsica.

Genus	Sardinia		Corsica		Total species
	No. of species	New record	No. of species	New record	
Dixa	?	0	7	0	7
Chaoborus	2	2	2	1	3
Anopheles	9	3	11	1	12
Uranotaenia ..	1	1	1	0	1
Culiseta	6	4	3	0	6
Orthopodomyia ..	1	1	0	0	1
Taeniorhynchus ..	1	1	2	0	2
Aëdes	9	5	12	1	12
Culex	6	3	8	0	8
TOTAL	35	20	46	3	52

In the treatment of genera, I have followed the sequence adopted by Edwards in the Genera Insectorum (1932). Subgenera have not been considered, and species are arranged alphabetically within the genus. Where locality records are listed, an asterisk (*) indicates collections of aquatic stages, otherwise they refer to adult insects. Wherever possible an attempt has been made to keep the keys simple; these for the most part are original, although sometimes it has been necessary to refer to the works of others. The same is true regarding descriptive notes of species; unless otherwise indicated, these are based on observation of material from the two islands. The revised nomenclature for the chaetotaxy of larvae and pupae proposed by Belkin (1950, 1952) has been adopted.

In the list of localities given under each species, the specimens were collected by the author and, or, H. Trapido where only a date is indicated.

FAMILY CULICIDAE.

The characters distinguishing the family CULICIDAE are largely to be found in the wing venation of the adult insect, the principal features, as outlined by Edwards (1932), being the following: subcosta (*Sc*) long and reaching costa; radius (*R*) 4-branched, R_1 (first longitudinal vein) simple, R_{2+3} (second longitudinal vein) forked, forming upper (anterior) fork cell, and R_{4+5} (third longitudinal vein) simple; no cross-veins connecting R_1 and R_2; media (M_{1+2}, fourth longitudinal vein) 2-branched, forming lower (posterior) fork cell; cross-veins *r-m* and *m-cu* both present; cubitus (Cu_{1+2}, fifth longitudinal vein) forked; anal (*An*, sixth longitudinal vein) long and reaching wing margin; and axial (*Ax*) absent or very faint.

The larvae are distinguished by the presence of a complete head capsule, and only one pair of functional spiracles (absent in the genus *Chaoborus*) which are located dorsally on the ninth abdominal segment. The immature stages are aquatic.

Representatives of all three subfamilies of the CULICIDAE are present in the islands and may be separated by stage according to the characters in the following keys (according to Edwards, 1932).

Keys to Subfamilies of CULICIDAE.

Larvae.

1. Thorax narrow, with distinct segmentation .... DIXINAE
   Thorax markedly broader, without distinct segmentation 2
2. Antennae prehensile, with long and strong apical setae. No external spiracular apparatus; instead, 2 pairs kidney-shaped air sacs, one in thorax and other in posterior abdomen .... CHAOBORINAE (*Chaoborus*)
   Antennae not prehensile. External spiracular apparatus present ... CULICINAE.

Pupae.

1. Paddles fused basally, not movable, without hairs or spines. Spiracle beyond middle of respiratory horn .... DIXINAE
   Paddles free, movable, hairs present 2
2. Respiratory horn almost closed apically .... CHAOBORINAE
   Respiratory horn open at tip, internal spiracle at its base .... CULICINAE.

Adults.

1. Head with antennal flagellum 14-segmented; mouth-parts short. Wing having subcosta ending above or before base of radial sector. No scales .... DIXINAE
   Head with antennal flagellum 13-segmented. Wing having subcosta ending much beyond base of radial sector 2
2. Head with mouth-parts short, palpi incurved. Scales confined almost entirely to wing fringe .... CHAOBORINAE
   Head with long proboscis, palpi not incurved. Scales on wing veins and legs .... CULICINAE.

Subfamily DIXINAE.

The Dixids or Dixa midges are small, practically hairless, flies differing from members of the other two subfamilies, among other things, by the absence of scales on the body or its appendages. Like the Chaoborids, the mouth-parts are short rather than developed into the long proboscis characteristic of mosquitoes. The antennae are long, bear short hairs and scarcely differ in the two sexes.

The eggs are laid in gelatinous masses on partially submerged rocks or other objects. The larvae lie at the surface of the water, like the Anophelines, usually assuming a characteristic "U"-shaped position. They move in a jerky fashion, extending first the front and then the back end of the body, travelling in the direction of the bent portion. Ordinarily they come to rest on top of emergent vegetation or some other exposed object, but remain immersed in the surface film. They are capable of doing this because of the presence of paired ventral pseudopods on the first two abdominal segments and paired, spiny plates on segments 5–7. The pupae are said to leave the water at the time of ecdysis. Dixid larvae are found in a variety of habitats, including pools, ponds, swamps, streams both flowing and stagnant, usually where there is an abundance of vegetation. The adults may be found nearby, resting under boulders and amid the vegetation.

Seven species have been reported from Corsica by Edwards (1928), one of which (*Dixa serrifera* Edw.), to my knowledge, is still known only locally. The others are common European species. Presumably, all or most of these species also occur in Sardinia. The following key is slightly modified from Edwards (1920*a*). For further information regarding these species, reference should be made to the papers by Edwards (1920*a*, 1928), Séguy (1923*b*) and Peus (1934*a*).

Genus Dixa.

Key to the Species of *Dixa*.

Adults.

1. Wings quite clear 2
   Wings clouded, at least on cross-veins and along basal part of 5th vein (*Cu*) 4
2. Head largely orange-brown in middle .... *autumnalis* (Mg.)
   Head mainly or entirely blackish or dark brown 3
3. Mesonotum mainly shining black. Head shining black .... *amphibia* Deg.
   Mesonotum anteriorly yellowish on sides. Head having front dark brown, dusted over with greyish; orange around nape .... *laeta* Lw.
4. Wings having dark spot over cross-veins small and rather ill-defined. Mesonotal middle stripe undivided. Pleurae mottled or unicolorous ... 5
   Wings having dark spot very large and sharply defined, spreading upwards almost to 1st vein (R_1). Mesonotal middle stripe usually divided. Pleurae distinctly striped 6
5. Thorax without grey shimmer. Pleurae nearly uniformly dark brown. Mesonotum with dark pubescence; pair of separate rounded dark spots anteriorly between the 3 dark stripes. Pronotal lobes entirely dark. Wing spot evenly spread around cross-vein .... *puberula* Lw.
   Thorax with grey shimmer on pale areas. Pleurae mottled. Mesonotum with pale pubescence; no separate round spots anteriorly. Pronotal lobes pale at sides. Wing spot mainly on inner side of cross-vein ... *submaculata* Edw.
6. Wings with bases of fork-cells not at all clouded .... *serrifera* Edw.
   Wings with bases of fork-cells conspicuously clouded .... *nebulosa* Mg.

There are at least seven species of *Dixa* in the islands. The species and their Corsican records, as given by Edwards (1928), are as follows:

Dixa autumnalis (Meigen).—Calvi.

Dixa laeta Loew (*fuscifrons* Edwards; see Peus, 1934*a*).—Abundant in marshes south of Biguglia.

Dixa amphibia De Geer.—South of Biguglia.

Dixa puberula Loew.—Abundant by mountain streams.

Dixa serrifera Edwards.—Common by mountain streams; Restonica valley and Valdoniello forest.

Dixa submaculata Edwards.—Together with *serrifera*.

Dixa nebulosa Meigen.—Ponte Leccia.

Subfamily Chaoborinae.

The Chaoborids are small inconspicuous gnats which ordinarily are infrequently seen. However, some species such as *Chaoborus astictopus* Dyar & Shannon, found at Clear Lake, California, may appear in enormous swarms at certain times and create a serious economic problem merely by their numbers. Like the Dixa midges, these gnats have short mouth-parts which are not adapted for blood-sucking. The antennae are hairy, those of the male being distinctly plumose. The Chaoborids have scales, as do the mosquitoes, but these are very scarce and are almost entirely confined to the wing fringe; there are some hair-like scales on the wing veins and a few scales on the posterior mesonotum may be present.

The eggs are laid on the surface of the water in a gelatinous matrix. The larvae have no external respiratory apparatus (*Chaoborus*) and live below the surface, usually in fairly deep water. They are called phantom or ghost larvae because of their transparent appearance, and when collected are detectable largely because of the two black eyes and two pairs of dark, kidney-shaped hydrostatic organs, one in the thorax and other in the posterior abdomen. The head is prolonged and snout-like, and the antennae are modified as prehensile organs for capturing prey, small crustaceans and mosquito larvae. They swim with a jerky movement, snapping their bodies back and forth. Like the larvae, the pupae remain below the surface, coming up only at the time of ecdysis. The adults are normally found resting or flying near the breeding places, but they are also attracted to light, to which they may come in enormous numbers.

Three species have been found in the islands, all belonging to the type genus. It is quite possible that the genus *Mochlonyx* is also present as it is widespread throughout the Holarctic region. The adults have the first tarsal segment much shorter than the second, whereas in *Chaoborus* it is longer. The pupae have a much shorter abdomen, rigid paddles and much less swollen respiratory horn. The larvae resemble those of *Chaoborus* in having prehensile antennae and hydrostatic organs, but differ in the possession of a respiratory siphon. For further information regarding this group, reference may be made to papers by Edwards (1920*a*. 1930), Séguy (1923*b*) and Peus (1934*b*).

Genus Chaoborus.

Keys to the species of *Chaoborus*.

Larvae.

1. Head with pre-labral appendages extremely slender (index of length to greatest width 16 : 1) (fig. 1) .... *pallidus* (F.)
   Head with pre-labral appendages much broader and more serrated (index not more than 6 : 1, more likely between 3 and 4 : 1) (fig. 1) 2
2. Mandible having 2nd (weak) tooth arising as branch of 3rd tooth; teeth generally darkened; mandibular fan having about 10 rays .... *crystallinus* (Deg.)
   Mandible with 2nd (weak) tooth arising exactly between 1st and 3rd teeth; teeth darkened apically only; mandibular fan having 13–15 rays .... *flavicans* (Mg.)

Pupae.

1. Respiratory horn greatly expanded in middle (index of length to greatest width about 3 : 1); apical spiracular opening greatly constricted and elongate. Paddle having " subterminal " hair of mid-rib single .... *pallidus* (F.)
   Respiratory trumpet more slender and elongate (index over 4 : 1); apical spiracular opening larger and short. Paddle having " subterminal " hair multiple 2

2. Paddle having ribs of outer and inner margins markedly thicker than middle rib; outer rib much shorter than middle rib and not toothed; much-branched hair tuft inserted about midway on middle rib or slightly distally .... *flavicans* (Mg.)

   Paddle having outer and middle ribs about same thickness basally and subequal in length; outer rib toothed distally; inner rib slightly thicker than others; much-branched hair tuft inserted at distal 2/3 of middle rib .... *crystallinus* (Deg.)

Adults.

1. Wing membrane with brown patch at cross-vein; 5th vein (Cu_2) with hairy spur near tip, parallel with hind margin of wing. Legs with light and dark areas giving appearance of rings .... *pallidus* (F.)

   Wing membrane not spotted; 5th vein running straight to hind margin, without spur. Legs unicolorous 2

2. Thorax having posterior pronotum blackish on upper half, yellowish on lower half. Antenna of male with last segment distinctly shorter than penultimate .... *crystallinus* (Deg.)

   Thorax having posterior pronotum either uniformly pale or else indistinctly darker on *lower* half in light specimens, or uniformly dark brown in dark specimens. Antenna of male with last 2 segments subequal .... *flavicans* (Mg.).

Chaoborus crystallinus (De Geer) 1776. Mémoires pour Servir à l'Histoire des Insectes. P. Hesselberg, Stockholm. **6,** p. 386 (*Tipula*).

I have not seen *crystallinus* and I have therefore relied on the literature for its description. It is a tiny grey gnat, apparently subject to considerable variation in coloration. It is easily separated from *Chaoborus pallidus* (F.) by the absence of spots on the legs and wings, the normal fifth longitudinal vein, and the presence of dark stripes on the thorax. The separation from *Chaoborus flavicans* (Mg.) is less evident (at least in females) and depends upon the coloration of the posterior pronotum and the relative lengths of the terminal segments of the male antenna (Edwards, 1920*a*, 1930; Séguy, 1924).

The larvae are easily identified by the form of the broad, leaf-like pre-labral appendages, which are markedly serrate on their anterior margins, and the mandibular fan and tooth arrangement. Likewise, the form of the respiratory trumpet and paddles of the pupa apparently are quite distinctive (Peus, 1934*b*). (*Note*: Larval specimens in the British Museum from Letchworth, England, have an 8-rayed mandibular fan.)

Breeding places.—The immature stages are found in the open water of ponds and lakes.

Sardinian localities.—None.

Corsican localities.—Calvi (Edwards, 1928).

Chaoborus flavicans (Meigen) 1818. Systematische Beschreibung der Bekannten Europäischen Zweiflügeligen Insekten. F. W. Forstmann, Aachen. **1,** p. 248 (*Corethra*).

I have not seen the adults of this species, but according to Edwards (1930) they are small, whitish or yellowish gnats, somewhat similar to *crystallinus*.

I originally took the two larvae before me to refer to *crystallinus* until I came across the paper by Peus (1934*b*); the placement of the second mandibular tooth as well as the number of rays in the mandibular fan (13) appear to me indicative of *flavicans*. Other characteristics of these larvae are as follows: antennal filaments (4 long and one short); post-antennal filaments (5 pairs); pre-labral appendage index 3·4 : 1 (fig. 1) and anal fan (21 rays). According to Peus, the pupae appear to be quite distinctive.

Breeding places.—Similar to those of *crystallinus*.

Sardinian localities.—Corongiu reservoir, Sinnai* (30.vi.50) (the larvae were in the Cagliari tap water coming from the reservoir).

Corsican localities.—None.

Chaoborus pallidus (F.) 1781. Species Insectorum, Exhibentes Eorum Differentias Specificas, Synonyma, Auctorum, Loca Natalia, Metamorphosin, Adjectis Observationibus, Descriptionibus. C. E. Bohn, Hamburgi & Kilonii. **2**, p. 407 (*Tipula*).

Like those of the other two species recorded from the islands, the adults of *pallidus* are very small gnats, opaque in colour, and characterised by having dark spots on the legs and a brown patch on the wing membrane in the area of the cross-vein (faint in males). Moreover, the posterior branch of the fifth vein has a pre-apical spur which is prolonged along the hind margin of the wing.

The larvae are distinguished by the very slender, inconspicuous pre-labral appendages (fig. 1), which have an index (length to greatest width) of 16 : 1; these appendages are fringed with fairly long filaments, particularly on the posterior margin. Other characters include the following: antennal filaments (4 long and one short); post-antennal filaments (5 pairs); mandibular fan (15 rays); and anal fan (21–22 rays). The pupae are recognised by their fat respiratory trumpets with the constricted apical opening. The paddles are somewhat similar to those of *flavicans* except that the " subterminal " hair of the mid-rib is single and inserted before the middle.

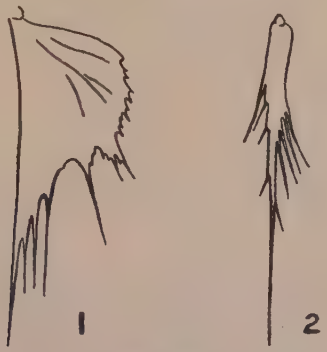


Fig. 1.—Pre-labral appendages of the larval head of (1) *Chaoborus flavicans* and (2) *C. pallidus*.

Breeding places.—Specimens found by the writer have been taken in small collections of water. The Corsican larvae came from a small, shaded depression (about 10 cm. deep) under a log along a river bank; associated with them were larvae of *Culex impudicus* Fic. Edwards (1920*a*) mentions that *pallidus* larvae are found among dense vegetation.

Sardinian localities.—Gonnosfanadiga* (8.iv.48).

Corsican localities.—Prunette (23.viii.44) and Solenzara* (25.viii.52).

Subfamily CULICINAE.

The true mosquitoes, as represented by species occurring in the islands, are characterised by a dense clothing of scales on the body (except in the Anophelines), the legs, wing veins and wing margins. The mouth-parts are prolonged, forming a slender proboscis for sucking blood or juices, and the male antennae are distinctly plumose. While the food habits of all the species are not definitely known, some are annoying pests of man and domestic animals (*e.g.*, *Aëdes detritus* (Hal.)), and at least two have been responsible for malaria transmission (*Anopheles l. labranchiae* Flni. and *A. sacharovi* Favr).

The eggs may be laid singly in damp soil (*Aëdes caspius* (Pall.) and *Culiseta fumipennis* (Steph.), the latter according to Marshall, 1938), in fissures of wood in tree holes (*Aëdes geniculatus* (Ol.)) and on the surface of open water (*Anopheles labranchiae* Flni. and *Aëdes mariae* (Ed. & Et. Serg.)), or bound together in small floating rafts (*Culex* spp., *Taeniorhynchus* spp. and *Culiseta annulata* (Schr.)). The larvae live in water but come to the surface to breathe (except for *Taeniorhynchus*, whose larvae and pupae obtain oxygen from submerged plant stems through their respiratory horns). Some species, if disturbed, may remain below the surface for long periods of time (*e.g.*, at least an hour and perhaps longer in the case of *Anopheles hispaniola* (Theo.)). The pupae are likewise air-breathing. The aquatic stages may be found in practically every type of water from rock pools of concentrated salt water along the coast (*e.g.*, *Aëdes mariae*) to rain-water collected in tree holes (*e.g.*, *Orthopodomyia pulchripalpis* (Rond.)). Some species breed throughout the year (*e.g.*, *Anopheles claviger* (Mg.)) and others pass the winter as semi-hibernating adults (*e.g.*, *A. labranchiae*) or in complete hibernation as eggs (*e.g.*, *Aëdes rusticus* (Rossi)), as larvae (*Anopheles plumbeus* Steph.) or as adults (*Anopheles marteri* Sen. & Prun.). The adults may be found in man-made shelters or else in natural resting places.

A total of 42 species of mosquitoes are known from the islands, but all are to be found in the nearby continental areas. While the present list is felt to be fairly complete, additional species may eventually show up, among which might be mentioned *Culex prosecutor* Séguy and the tree-hole breeding *Aëdes echinus* Edw.

Key to Genera of CULICINAE.

Larvae.

1. Breathing siphon absent. Abdominal tergites with palmate hair tufts at least on segments 3–6 .... ANOPHELES

   Breathing siphon present. Abdominal tergites without palmate hair tufts ... 2

2. Siphon without pecten. Abdominal tergites 6 or 7–8 with dorsal, sclerotized plates (mature larvae) .... ORTHOPODOMYIA (*O. pulchripalpis* (Rond.))

   Siphon with pecten. Abdominal tergites without dorsal plates. (Note: see *Uranotaenia*) 3

3. Abdomen having comb spines of 8th segment united on lateral sclerotic plates .... URANOTAENIA (*U. unguiculata* Edw.)

   Abdomen with comb spines or scales not arising from lateral plates 4

4. Siphon short, with apex prolonged into cutting apparatus for piercing plant tissues. Antennae very long, much longer than head, portion distal to tuft about double basal portion .... TAENIORHYNCHUS

   Siphon longer and not equipped for piercing plants. Antennae shorter than head; if longer, portion distal to tuft shorter than basal portion 5

5. Siphon with 8 or more hair tufts .... CULEX

Siphon usually with 2 hair tufts (Note: *Aëdes rusticus* has some supplementary single hairs dorsally as well as a pair of lateral accessory tufts) 6

6. Siphon hair tufts situated at base of siphon .... CULISETA

Siphon hair tufts usually situated at middle or towards apex of siphon, never at extreme base .... AËDES.

Adults.

1. Palpi of females about as long as proboscis. Abdomen not clothed with scales (few scales on 7th sternite and 8th tergite in *hyrcanus*) ... ANOPHELES

Palpi of females $\frac{1}{3}$ or less length of proboscis (about $\frac{1}{2}$ in *Orthopodomyia pulchripalpis*). Abdomen densely clothed with scales 2

2. Wings with 6th vein (*An*) ending a little before fork of 5th vein (*Cu*); fork cells of 2nd (R_{2+3}) and 4th (M_{1+2}) veins less than $\frac{1}{2}$ as long as their stems .... URANOTAENIA (*U. unguiculata* Edw.)

Wings with 6th vein ending well beyond fork of 5th vein; fork cells of 2nd and 4th veins as long or longer than their stems 3

3. Thorax with spiracular bristles present. Wings having underside of base of costal vein hairy .... CULISETA

Thorax without spiracular bristles. Wings without hairy patch on underside of base or costal vein 4

4. Tarsi of fore-legs with 4th segment no longer than broad. Palpi of females about $\frac{1}{2}$ length of proboscis. Mesonotum with 6 white lines .... ORTHOPODOMYIA (*O. pulchripalpis* (Rond.))

Tarsi of fore-legs with 4th segment distinctly longer than broad. Palpi of females about $\frac{1}{5}$ or less length of proboscis. Mesonotum otherwise 5

5. Thorax with post-spiracular bristles present. Abdomen of female apically pointed .... AËDES

Thorax with post-spiracular bristles absent. Abdomen of female apically rounded 6

6. Hind tarsi having 1st segment as long or longer than tibia (shorter in *modestus*). Wing scales narrow. Legs with pulvilli .... CULEX

Hind tarsi having 1st segment distinctly shorter than tibia. Wing scales broad and conspicuous. Legs without pulvilli .... TAENIORHYNCHUS.

Genus ANOPHELES.

Key to the species of *Anopheles*.

Eggs.

1. Floats absent or rudimentary 2

Floats well developed 5

2. Marginal frill reduced to small oval pre-apical dorsal spot. Egg banana-shaped .... *hispaniola* (Theo.)

Marginal frill surrounding dorsal surface. Eggs slightly convex dorsally or markedly concave 3

3. Egg diamond-shaped. Marginal frill broad and conspicuous .... *plumbeus* Steph.

Egg elongate 4

4. Marginal frill conspicuously broad (about ½ dorsal egg width). Dorsum markedly concave and black .... *superpictus* Grassi
   Marginal frill narrow. Dorsum slightly convex and frosty-white (rudimentary floats in early spring eggs) .... *sacharovi* Favr
5. Marginal frill not interrupted by floats .... *hyrcanus* (Pall.)
   Marginal frills interrupted by floats 6
6. Dorsum with light and dark areas 7
   Dorsum uniformly dark (occasionally with few pale patches in *melanoon*) ... 10
7. Float membrane smooth except for few corrugations at extremities. Floats generally in middle, encroaching on to dorsum, occupying not more than 35 per cent. of egg length, about 18 ribs .... *atroparvus* van Thiel
   Float membrane rough 8
8. Floats small, occupying less than 20 per cent. of egg length, placed well towards one end, not extended on to dorsal surface, about 14 ribs. Dorsum with dark lateral cuneiform spots or irregular bands .... *labranchiae* Flni.
   Floats large, occupying 40–50 per cent. of egg length, centrally located, extended somewhat on to dorsal surface, about 20 ribs. Dorsum with conspicuous subterminal transverse bars 9
9. Dorsum light grey except for extremities and transverse bars .... *maculipennis* Mg. *s.str.*
   Dorsum with diffuse dark pattern .... *messeae* Flni.
10. Egg narrow, sharply pointed at both ends and shiny black. Ends of floats curved on to dorsal surface as handlebar projections; float membrane smooth .... *algeriensis* Theo.
    Egg broad, bluntly pointed and dull. Ends of floats not curved on to dorsal surface 11
11. Dorsum broad. Floats occupying about 35 per cent. of egg length, smooth, about 18 ribs .... *melanoon* Hackett
    Dorsum narrow due to encroaching floats which are very large and occupy 50 per cent. or more of egg length 12
12. Floats occupying about 50 per cent. of egg length; membrane smooth .... *claviger* (Mg.)
    Floats occupying about 75 per cent. of egg length; membrane moderately rough .... *marteri* Sen. & Prun.

Larvae (1*st instar*).

1. Head having subantennal hair much branched 2
   Head having subantennal hair bifurcate 3
2. Subantennal hair asymmetrically pinnately branched; shaft relatively weak .... *maculipennis* group
   Subantennal hair symmetrically branched and arboriform (*i.e.*, secondary branchlets); shaft strong .... *hyrcanus* (Pall.)
3. Subantennal hair much shorter than antenna, apically branched. Clypeal hairs with fine branches .... *plumbeus* Steph.
   Subantennal hair long, basally branched. Clypeal hairs usually simple ... 4
4. Subantennal hair about as long as antenna 5
   Subantennal hair much longer than antenna 6

5. Subantennal hair with more or less straight branches (not recurved). Inner clypeal hairs closer to outer clypeals than to each other ... *hispaniola* (Theo.)

Subantennal hair with branches apically curved at an angle. Inner clypeal hairs closer to each other than to outer clypeals .... *claviger* (Mg.)

6. Subantennal hair strongly recurved. Terminal antennal hair less than double length of terminal spines or sabres .... *marteri* Sen. & Prun.

Subantennal hair weakly recurved. Terminal antennal hair double or more the length of sabres .... *algeriensis* Theo.

Larvae (4th instar).

1. Head with frontal hairs very short and simple; subantennal hairs very short and 2- to 3-branched; antennae without spines. Abdominal segments 1–6 with lateral hairs pinnately branched .... *plumbeus* Steph.

Head with frontal hairs long and much branched; subantennal hairs nearly as long as antennae and pinnately branched; antennae spinose. Abdominal segments 1–3 with lateral hairs pinnately branched (Note: segments 1–5 in *hispaniola*) 2

2. Head with inner clypeal hairs closer to outer clypeal hairs than to each other; antennal shaft hairs simple and minute 3

Head with inner clypeal hairs closer to each other than to outer clypeal hairs; antennal shaft hairs conspicuous and much branched 4

3. Head having frontal hairs poorly developed, with *few* branches, *all arising near base* of shaft. Abdominal segments 4 and 5 with lateral hairs pinnately branched .... *hispaniola* (Theo.)

Head with frontal hairs having well-developed, long shaft, pinnately branched throughout. Abdominal segments 4 and 5 with lateral hairs 2- to 4-branched from near base .... *superpictus* Grassi

4. Head with outer clypeal hairs simple, or with few minute branchlets (with 2 or 3 branches in *claviger*) 5

Head with outer clypeal hairs much branched 7

5. Head with fronto-clypeus having 3 transverse bands; clypeal hairs with few minute branchlets along shaft; inner occipital (sutural) hair tuft with about 4 apical branches. Abdominal segments 4 and 5 with well-developed "0" hair, 4- to 5-branched; dorsal plates of segments large, at least 5–6 times as wide as long .... *algeriensis* Theo.

Head with fronto-clypeus spotted but not banded. Clypeal hairs simple (rarely with 2–3 apical branches in *claviger*); inner occipital hairs simple or bifurcate at base. Abdomen with "0" hair absent or minute and simple; dorsal plates small, not more than 3 times as wide as long 6

6. Thorax with inner submedian prothoracic hair having weakly developed shaft with 3–4 apical branches. Abdomen with palmate hair leaflets only slightly serrated and not terminating in long filament .... *claviger* (Mg.)

Thorax with inner submedian prothoracic hair having strong shaft, pinnately branched similar to middle hair. Abdomen with palmate hair leaflets distinctly toothed and terminating in long pseudofilament .... *marteri* Sen. & Prun.[1]

---

[1] Langeron & Galliard (1933) report an unusual third-instar Anopheline larva from Corte, Corsica, which they were unable to identify. Its essential characteristics are as follows: anterior clypeal (inner and outer), posterior clypeal and inner occipital (sutural) hairs unbranched. Inner clypeals close together. Antennal shaft hair branched. Palmate hair leaflets of metathorax and abdominal segments with very long filaments, longer than basal

7. Head with inner clypeal hairs having short apical branches; antennal shaft tufts arising about midway on antennae .... *hyrcanus* (Pall.)

   Head with inner clypeal hairs having long apical branches; antennal shaft tufts arising near base of antennae (basal ⅓ to ¼) 8

8. Abdominal segments 4 and 5 with the *four* antepalmate hair tufts *together* having the following mean number of branches:[2]

   (a) Mean 9·63; standard deviation 1·85; range 4–13 ... *labranchiae* Flni.

   (b) Mean 10·80; standard deviation 1·62; range 7–16 .... *atroparvus* van Thiel

   (c) Mean 13·05; standard deviation 1·35; range 10–17 ... *maculipennis* Mg. *s.str.*

   (d) Mean 14·82; standard deviation 2·40; range 11–21 ...... *messeae* Flni.

   (e) Mean 24·49; standard deviation 3·30; range 16–32 ...... *melanoon* Hackett

   (f) Mean 30·78; standard deviation 4·29; range 19–39 ... *sacharovi* Favr.

Pupae.

1. Abdominal segment 8 having lateral spine long and simple .... *plumbeus* Steph.

   Abdominal segment 8 having lateral spine short and branched 2

2. Paddle margins completely fringed with long hairs; terminal seta strong and conspicuous .... *marteri* Sen. & Prun.

   Paddle margins only partially fringed with hairs (usually short) or teeth ... 3

3. Paddle having external posterior margin fringed with prominent widely-spaced teeth; terminal seta long, robust and strongly hooked .... *hispaniola* (Theo.)

   Paddle having posterior half of external margin fringed with hairs or fine teeth 4

4. Paddle having terminal seta long, robust and strongly hooked; posterior ⅓ of external margin of paddle fringed with fairly long hair .... *superpictus* Grassi

   Paddle having terminal seta usually shorter, straight or slightly curved, simple or branched; paddle fringed with shorter hairs or tiny teeth 5

5. Paddle terminal hair branched (2- to 3-branched or more) 6

   Paddle terminal hair normally simple (occasionally 2-branched) 7

6. Abdominal segment 7 having hairs 1 and 4 (C and B of authors) simple or with few branches. Respiratory horn normal shape[3] ...... *sacharovi* Favr

   Abdominal segment 7 having hairs 1 and 4 with many branches. Respiratory horn short and wide, meatus ½ as long as total horn length[3] .... *hyrcanus* (Pall.)

7. Abdominal segment 7 having lateral spine short and blunt. Paddle having fine hairs on posterior external margin extending to terminal seta .... *labranchiae* Flni.

   Abdominal segment 7 having lateral spine long and tapering to sharp point 8

---

portion of leaflets which have a few jagged serrations. These characters suggest *marteri*, except that in the latter species the metathoracic palmate leaflets do not have serrations and those of the abdominal segments have shorter filaments and more serrations.

[2] From Bates (1939); based on counts of 100–154 larvae from various regions (Italy, Albania, Hungary and Germany).

[3] According to Buxton (1924).

8. Paddle having posterior half of both external and internal margins fringed with fine hairs; subterminal hair 4- to 6-branched and not reaching paddle margin .... *algeriensis* Theo.

Paddle having posterior half of *only* external margin fringed, with even finer hairs, but not reaching to terminal hair; subterminal hair usually single and reaching paddle margin .... *claviger* (Mg.).

Adults.

1. Wings not spotted 2

Wings spotted 5

2. Head dark. Mesonotum unicolorous, reddish-brown, with dark hair .... *algeriensis* Theo.

Head with pale frontal tuft. Mesonotum with pale central stripe and dark sides; pale hair medianly and tuft of pale scales anteriorly 3

3. Wings with pale apical fringe. Fore-leg having tarsal segment 1 distinctly longer than segments 2–5 .... *marteri* Sen. & Prun.

Wings completely dark. Fore-leg having tarsal segment 1 shorter or equal to segments 2–5 4

4. Palpi of female having apical segment less than ½ as long as penultimate. Head and anterior margin of mesonotum with clump of creamy or yellowish-white scales .... *claviger* (Mg.)

Palpi of female having apical segment ½ as long as penultimate or more. Head and anterior margin of mesonotum with clump of pure white scales .... *plumbeus* Steph.

5. Wings with light and dark scales forming patches of colour 6

Wing scales all dark, except for pale apical fringe in some species 8

6. Wing having costal margin interrupted by 2 pale areas in the apical half. Proboscis and palpi shaggy. Bases of front femora enlarged .... *hyrcanus* (Pall.)

Wing having costal margin interrupted by 5 pale areas. Proboscis and palpi not shaggy nor femora enlarged 7

7. Palpi usually with apex dark .... *hispaniola* (Theo.)

Palpi usually with apex pale .... *superpictus* Grassi

8. Mesonotum and wing unicolorous. Wing spots less distinct ... *sacharovi* Favr

Mesonotum with pale central stripe. Wings with pale apical fringe frequently evident; spots distinct (less so in males) 9

9. Wing having plume scales of 2nd vein slender and tapering gradually towards the tip .... *atroparvus* van Thiel
labranchiae Flni. ?

Wing having plume scales of 2nd vein wider and tapering differently 10

10. Wing having plume scales of 2nd vein tapering acutely towards the tip ...... *messeae* Flni.

Wing having plume scales of 2nd vein wider than in *messeae* and tapering less acutely towards the tip .... *maculipennis* Mg. *s.str.*

Males.

1. Basistyle with 4–7 parabasal spines; internal spine absent 2

Basistyle with 1–3 (usually 2) parabasal spines; conspicuous internal spine on inner margin of basistyle 3

2. Basistyle with 5 long parabasal spines, one of the anterior group of 4 being much stouter than the others, the posterior 5th spine being extremely long, almost length of basistyle (index 1 : 1·25) .... *superpictus* Grassi

Basistyle with 4–7 (usually 6) short parabasal spines, all more or less the same size and length .... *hispaniola* (Theo.)

3. Basistyle with one parabasal spine; internal spine inserted near apex .... *algeriensis* Theo.

Basistyle with 2–3 parabasal spines 4

4. Basistyle with 3 parabasal spines, one being simple and the other 2 apically branched; internal spine inserted near apex .... *claviger* (Mg.)

Basistyle with 2 parabasal spines; internal spine inserted nearer the middle 5

5. Phallosome without leaflets. Parabasal spines approximately same length ... *plumbeus* Steph.

Phallosome with leaflets at apex. Parabasal spines unequal, outer spine longer 6

6. Claspette having outer lobe bearing 3 flattened spatula-like setae and inner lobe a longer flattened sabre-like seta. Parabasal spines arising from a strongly sclerotized base .... *marteri* Sen. & Prun.

Claspette otherwise. Parabasal spines not inserted in a sclerotized base ... 7

7. Claspette having spines *fused* into a flattened spatula-like process on outer lobe and 2 simple pointed setae on inner lobe .... *hyrcanus* (Pall.)

Claspette lobes not well defined, external spine(s) pointed, blunt or rounded but not fused together (*maculipennis* group) 8

8. (a) Claspette external spine(s) variable, 50 per cent. acute but of almost equal width throughout, about $\frac{2}{3}$ length of apical spine ... *sacharovi* Favr

(b) Claspette external spine(s) very sharp and tapering evenly from base to tip; single 50 per cent. of time .... *labranchiae* Flni.

(c) Claspette external spine(s) short, medium or long; sharp, blunt or rounded (usually blunt); tapers little from base to apex and when pointed sharpens suddenly just below the tip .... *melanoon* Hackett, *messeae* Flni.

(d) Claspette external spine(s) very sharp and tapering evenly from base to tip; spine usually double .... *atroparvus* van Thiel

(e) Claspette external spine(s) blunt or round and of almost uniform width throughout; length variable .... *maculipennis* Mg. *s.str.*

Anopheles algeriensis Theobald 1903. A Monograph of the Culicidae or Mosquitoes. The British Museum (Natural History), London. **3**, p. 21.

This is a somewhat russet-coloured species, characterized by the absence of markings or pale scales on the mesonotum, dark head and unspotted wings. The male terminalia are notable for the presence of only one parabasal spine, but like *claviger* have the internal spine inserted near the apex of the basistyle.

The mature larvae are easily recognized by a variety of characters summarized in the key. Among these, the exceptional development of the " zero " hair on the antero-lateral areas of the abdominal tergites (first noted by La Face, 1929) should be pointed out; apparently this character has been overlooked by most workers. The first-instar larvae resemble those of *marteri* and *claviger* but can be identified with fair success by the form of the terminal antennal (4) and subantennal (11) hairs. La Face (1929) says the four anterior clypeal hairs are equidistant from each other; however, I have not found this always to be the case; the inner pair sometimes being farther apart.

The pupae are readily separated by the characters covered in the key. In addition, the shape of the paddles is distinctive, being elongate, somewhat sinuous and bluntly pointed.

Likewise, the eggs are not to be confused with those of other species recorded from the islands because of their distinctive shape, colour and floats. (See also La Face, 1929.)

Breeding places.—The larvae are primarily found in sluggish streams and rivers. Marshes are also suitable habitats, particularly in the cooler months. Clear, fresh water, usually still and partially shaded, characterizes the breeding places. Particularly in the winter months, however, larvae may be well hidden, as for example at the bases of *Juncus*.

Sardinian localities.—Portotorres (Missiroli, 1927). Widespread throughout the island, essentially in lowland areas. Common in the north-west (Nurra) and along the south-west coast; also found in the islands of Sant'Antioco, San Pietro and Caprera. Second only to *claviger* in abundance.

Corsican localities.—Padulone, near Cateraggio (Brumpt, 1925); Vico (Catanei, 1925). Fairly widespread in the lowlands (Jaujou & others, 1950, 1951).

Anopheles claviger (Mg.) 1804. Klassifikazion und Beschreibung der Europäischen Zweiflügeligen Insekten (Diptera). Karl Reichard, Braunschweig, Germany. **1**, p. 4 (*Culex*).

While not infallible, the characters indicated in the key should serve to distinguish most adults of this species. The difficulty is increased by the fact that *claviger*, *marteri* and *plumbeus* are all sylvan species and hence the adults are likely to be found in the same type of resting places; of the three, *claviger* is most apt to come into man-made shelters. The male terminalia with their three parabasal spines (two of which are apically much branched) are highly distinctive.

In addition to the larval characters in the key, mention should be made of the form of the subantennal hair (11) of the mature larva; the shaft (when seen flat) has a coarse apical bifurcation bearing many dendritic branchlets. The first-instar larvae are recognised by the length and form of the subantennal hair as well as by the spacing of the anterior clypeal hairs, although this is not always easily done.

The pupae are readily identified by the characters indicated in the key. The same is true for the eggs.

I have not attempted to differentiate any of the so-called varieties of *claviger*, but *petragnani* Del Vecchio has been reported from Corsica (Jaujou & others, 1950); for further information see Del Vecchio (1939) and Torres Cañamares (1945).

Breeding places.—The larvae of *claviger* are found in a wide variety of habitats, but show a preference for small water courses, usually heavily shaded and cool.

Sardinian localities.—Sardinia, as *Anopheles bifurcatus* (Linn.) by Ficalbi (1899); Portotorres, as *bifurcatus* (Missiroli, 1927). *A. claviger* occurs throughout the island from sea level to at least 1,300 metres; it is the most abundant Anopheline now found in the island.

Corsican localities.—Vico, Evisa, Corte, Orezza and Zalana (Catanei, 1925); Biguglia (Edwards, 1928); numerous localities along the coast and in the interior seen by me in 1944, also more recently by Jaujou & others (1950, 1951) who report it as being practically the only Anopheline seen above 600 metres; highest elevation found, 1,160 metres.

Anopheles hispaniola (Theobald) 1903. A Monograph of the Culicidae or Mosquitoes. The British Museum (Natural History), London. **3**, p. 49 (*Myzomyia*).

The adults are recognised by the many light and dark areas on the wings and the banded palpi. Normally the latter has three narrow, pale rings at joints 2–3, 3–4 and 4–5, with the greater part, including the apex of the terminal segment, dark; sometimes, however, the very tip may be white but the middle of the terminal segment remains dark. In such cases, the species is apt to be confused with some individuals of *superpictus* from which it may be separated by the apical pale band of the palpus being narrower than the pre-apical pale band, as well as the mesonotal scales being uniformly narrow and hair-like; in *superpictus*, the apical band of the palpus (if present) is much wider and the scales of the mesonotal margins are broader and straighter. The male terminalia are also similar to those of *superpictus* but differ in the number and shape of the parabasal spines.

The mature larvae are rècognised by the widely spaced inner clypeal hairs, weakly developed frontal hairs with basal branching only, and the pinnately-branched lateral hairs (6) of abdominal segments 1–5 (weakly pinnate on 4 and 5). In addition, the mesothoracic pleural hairs (9, 10) are both branched. The terminal filaments of the palmate hair leaflets are not as long as in *superpictus*. Palmate hairs are present on segments 2–7, those on 2 being weakly developed. The first-instar larvae are fairly readily identified by the characters mentioned in the key.

The pupae are unique amongst those of Anophelines found in the islands in having conspicuous, widely spaced teeth on the exterior margin of the posterior half of the paddles; these teeth become hair-like just before reaching the terminal seta, which is long, stout and terminally hooked. The internal margin of the paddle (beyond the terminal seta) is bare of teeth or hairs. The subterminal seta is simple, short and inserted fairly close to the terminal seta, so that it almost reaches the posterior margin of the paddle. As in *superpictus* the lateral spine of the 6th and 7th segments is very long, more than ½ the length of the succeeding segment.

The eggs are small and dark bluish-grey in colour. They are bluntly rounded at the enlarged micropylar end, more pointed at the other, and curved somewhat like a banana. The exochorion has a hexagonal pattern and completely covers the egg except for a rosette-shaped black area around the micropyle. There are no floats, and the appressed " marginal " frill is reduced to a small oval-shaped dorsal spot adjacent to and touching the micropylar area.

Breeding places.—The preferred larval habitats of the Sardinian *hispaniola* are sandy or gravelly stream beds; shallow, well-aerated water containing *Spirogyra* and water cress.

Sardinian localities.—Unknown from the island prior to ERLAAS. Occurring widely, except in the far north, but most common in the south-eastern mountain mass from about midsummer on.

Corsican localities.—None. The absence of this species is strange as considerable collecting has been done in the island during recent years in the course of malaria control activities. On the other hand, it did not show up in Sardinia in numbers until the *labranchiae* population had been greatly reduced by intensive insecticidal operations. *A. labranchiae* occupied the same habitat as *hispaniola* and presumably masked the presence of the latter.

Anopheles hyrcanus (Pallas) 1771. Reise durch Verschiedene Provinzen des Russischen Reichs. Kayserliche Academie der Wissenschaften, St. Petersburg. **1**, p. 475 (*Culex*).

I have not seen this species, so have relied on the works of others for its description (Edwards, 1921; La Face, 1929; Christophers, 1933; and Senevet, 1935). Adults of *hyrcanus* are distinctive for their shaggily scaled proboscis and palpi, swollen base of anterior femora and spotted wings. The palpi are apically pale and have pale rings at joints 2–3, 3–4 and 4–5. The wings have two spots of pale scales on the distal half of the costal margin, the more proximal extending down to the first vein and the more distal to the lower fork of the fourth vein; two pale spots are also present on the sixth (anal) vein and the fringe at the wing apex is pale. The wings, however, are subject to considerable variation in their markings. The tarsi are apically pale except for the terminal segment which is completely dark. The variety *pseudopictus* Grassi, which occurs in Italy, is said to have the fourth tarsal segment of the hind leg completely pale; inasmuch as Brumpt (1925) found the Corsican form to resemble *sinensis* Wied. rather than *pseudopictus*, I am treating the species as similar to the type form. The male terminalia are readily distinguished from local Anophelines by the number of parabasal spines and the fused spatula-like spines of the outer claspette lobe.

According to La Face, the inner clypeal hairs of the mature larva have much shorter and finer apical branches than those found in larvae of the *maculipennis* group. Furthermore, the subantennal hairs (11), while pinnately branched, continue to have the arboriform (secondary branching) effect of the earlier stages. The first-instar larvae, according to this author, are easily identified by the stout-shafted subantennal hair with its arboriform branching. Other characters are as follows: the inner clypeal hairs are closer to each other than to the outer clypeals (opposite of the condition found in the *maculipennis* group), the post-clypeals are apically bifurcate, the frontal hairs are pinnately branched and the inner occipital hairs (8) are 2- to 3-branched.

The pupae apparently resemble somewhat those of *sacharovi*, but differ in the shape of the respiratory trumpet and the branching of the long apical hairs (1 and 4, C and B of authors) of the seventh segment. Like the latter species as well as *labranchiae*, the lateral spine of the seventh segment is somewhat short and blunt.

The egg has been figured by Edwards and appears to be quite distinctive.

Breeding places.—Generally found in extensive coastal marshes, also rice fields.

Sardinian localities.—Sardinia (Senevet, 1935). While it is possible that the species was present in the island, it was never seen during the period of ERLAAS.

Corsican localities.—Padulone, near Cateraggio (Brumpt, 1925); Porto Vecchio* and Propriano* (Toumanoff and Rageau, 1949); Lower Tavignano river, Cateraggio* (Jaujou & others, 1950). I have a record of a badly damaged female from Borgo (30.vi.44) which may be *hyrcanus*. The species is apparently very uncommon, at least in its association with man.

Anopheles maculipennis Group.

Under this heading I include five species and one subspecies which have been reported from both islands. These are *Anopheles maculipennis s.str.*, *A. labranchiae atroparvus*, *A. labranchiae labranchiae*, *A. melanoon*, *A. messeae* and *A. sacharovi*. The inclusion of *atroparvus* is dubious and I am inclined to believe it is not present in the islands, although Spanedda (1940) reported seven ovipositions from southern Sardinia; the Corsican record does not refer specifically to *atroparvus*, but to mosquitoes of the *atroparvus-labranchiae* type and was based on male terminalia (Galliard & Sautet, 1934*a*). Typical *maculipennis* has been reported only once from Sardinia (Hackett & Missiroli, 1935; one oviposition) and twice from Corsica (Galliard & Sautet, 1934*a*, 1935). Somewhat similarly, *messeae* has only the one record from Sardinia (Hackett & Missiroli, 1935; four ovipositions), but has been observed on several occasions in Corsica (Galliard & Sautet, 1934*a*,*b*, 1935; and Jaujou & others, 1950). The remaining three species, however, form a definite part of the fauna of the islands. *A. labranchiae*, at least formerly, was the most abundant species of the group as well as possibly of the entire mosquito population (in Sardinia). *A. sacharovi* has and had a very limited distribution in Sardinia but is more common in Corsica, and *melanoon*, while quite widely found, has never been frequent in collections.

The species comprising the European *maculipennis* group are not always easy to differentiate, and identification has been based largely on characters of the eggs (markings of the dorsal exochorion, presence of floats and their size, position and texture). This has meant collecting females and segregating them individually in oviposition vials or else searching for eggs in nature. The mature larvae of some species are readily identified by the number of branches of the antepalmate hairs (hair 2) of the fourth and fifth abdominal segments (best expressed as the total number of branches of the four hairs), but others show an overlapping in this character (Bates, 1939). Fortunately *labranchiae* and *sacharovi* lie at the opposite extremes in hair-branching, and *melanoon* is somewhat intermediate in position although overlapping somewhat with *sacharovi*. Little has been done with first-instar larvae and pupae, and I have not attempted to distinguish species except in the case of the pupae of *sacharovi* and *labranchiae*. In Sardinia, the pupae of the latter were likely to be confused only with those of *claviger* (excluding *melanoon*, which was very uncommon), particularly if the lateral spines were broken; they could be recognised, however, by the zone of external paddle fringe-hairs extending to the terminal seta and sometimes slightly beyond. van Thiel (1941) has attempted to differentiate the pupal stages based on the form and colour of the lateral spines of the sixth and seventh segments; except for general groupings of species, the distinctions are too nebulous for satisfactory application.

In the case of adults, again it is *sacharovi* which is most readily distinguished by coloration of the mesonotum and wing characters. Ungureanu and Shute (1947) as well as Laven (1950) have demonstrated slight differences in the type of plume scale on certain wing veins which may be of value in classification; the former observations have been included in the present key. It might be noted in passing that specimens presumed to be *labranchiae* have plume scales on the second vein similar to those of *atroparvus*; however, the latter subspecies has not been available for comparison. Somewhat variable differences have also been observed in the male terminalia; the characters incorporated in the key are based on the literature, largely taken from the papers of Hackett & Missiroli (1935) and Ungureanu & Shute (1947). Specific differences also exist in chromosomal pattern and biology, but they will not be discussed here.

Anopheles labranchiae atroparvus van Thiel 1927. Bulletin de la Société de Pathologie Exotique, **20,** p. 389 (*Anopheles maculipennis* Meigen var. *atroparvus*).

Breeding places.—The larvae are generally found in cool waters of moderate salinity not exceeding 10 parts per 1,000 of sodium chloride (Hackett & Missiroli, 1935).

Sardinian localities.—Presence doubtful. Campidano of Cagliari (Spanedda, 1940).

Corsican localities.—Presence doubtful. East coast (Galliard & Sautet, 1934*a*).

Anopheles labranchiae labranchiae Falleroni 1926. Rivista di Malariologia, **5,** p. 564 (*Anopheles claviger* Mg. var. *labranchiae*).

Breeding places.—The larvae are found in both fresh and saline waters ordinarily not exceeding 10 parts per 1,000 of sodium chloride, and prefer sunny exposures (Hackett & Missiroli, 1935). In Sardinia, *labranchiae* limited itself almost entirely to fresh waters where it was found in almost every type of habitat except the very densely shaded. The situation in Corsica is somewhat similar although the species does not seem to have invaded the higher mountain areas to the same extent as in Sardinia.

Sardinian localities.—Originally reported from the island by Ficalbi (1899) as *Anopheles claviger* (F.); probably refers to this species. Ubiquitous from sea level up to 1,000 metres in the pre-ERLAAS period, but now restricted to a few isolated coastal areas.

Corsican localities.—The early report of *Anopheles claviger* by Laveran (1900) from the vicinity of Bonifacio probably refers to *labranchiae* as it is the most common member of the *maculipennis* group in the islands. Found on the east coast (Galliard & Sautet, 1934*a*, *b*, 1935). Largely coastal in distribution, but does extend up the river valleys to moderate elevations (Jaujou & others, 1950).

Anopheles maculipennis *s.str.* Meigen 1818. Systematische Beschreibung der Bekannten Europäischen Zweiflügeligen Insekten. F. W. Forstmann, Aachen. **1,** p. 11.

Breeding places.—Largely occurring in cold pure water of upland areas, but also found in coastal zones usually associated with running streams (Hackett & Missiroli, 1935).

Sardinian localities.—Presence doubtful. Sardinia (Hackett & Missiroli, 1935).

Corsican localities.—East coast, Borgo (Galliard & Sautet, 1934*a*, 1935).

Anopheles melanoon melanoon Hackett 1934. Transactions of the Royal Society of Tropical Medicine & Hygiene, **28,** p. 113 (*Anopheles maculipennis* var. *melanoon*).

Breeding places.—In the islands, *melanoon* has been found in fresh-water ground pools, streams and water holes; sunny exposures in the springtime and more shady situations during the summer. Elsewhere, Hackett & Missiroli (1935) report it breeding in rice fields.

Sardinian localities.—Campidano of Cagliari (Spanedda, 1940); Muravera area*, Monastir*, Sardara*, Senorbi*, Isili*, Assolo*, Curcuris*, Padria*, Olmedo*, and Castel Sardo* (1946–1950).

Corsican localities.—Casabianda* (Galliard & Sautet, 1934*b*), Ghisonaccia (8.vi.44), Bravona* (16.vi., 18.ix.44; 25.viii.52), Porto Vecchio (24.vi.44; 26.viii.52*); Cateraggio, Poretta, Toga, Macinoggio, Meria (Jaujou & others, 1950).

Anopheles messeae Falleroni 1926. Rivista di Malariologia, **5**, p. 564 (*Anopheles claviger*, Mg. var. *messeae*).

Breeding places.—The larvae appear to prefer cool, fresh, standing waters (Hackett & Missiroli, 1935).

Sardinian localities.—Presence doubtful. Sardinia (Hackett & Missiroli, 1935).

Corsican localities.—East coast, Borgo (Galliard & Sautet, 1934*a*, *b*,* 1935); Mignattaja, Padulone, Poretta, Toga (Jaujou & others, 1950).

Anopheles sacharovi Favr 1903. An attempt to study malaria in Russia from the point of view of sanitation. Kharkov. p. 189 (In Russian).

Breeding places.—The larvae tolerate both fresh and saline waters up to concentrations of 24 parts per 1,000 of sodium chloride, but seem to prefer one or the other in certain parts of the species' range. Sunny exposures and abundant surface vegetation are usual characteristics of the habitats (Hackett & Missiroli, 1935). In Sardinia, *sacharovi* has been taken in coastal swamps, lagoons and nearby streams. The writer once found it together with *labranchiae* and *melanoon* in a Corsican fresh-water well containing algae and exposed to the sun.

Sardinian localities.—Siniscola and Portotorres (laboratory records of Professor Missiroli, 1932–1933); Porto Corallo (Spanedda, 1940); Barabisa swamp, Palau* (24.v.52), Lake Barazza, Alghero* (11.vi.52), Leccari swamp, Portotorres* (18.vi.52), Bonifica di Puzzinosi, Stintino* (3.vii.52), Pilo lagoon, Stintino* (16–17.vii.52) and Golfo di Saline, Palau* (22.vii.52). With the exception of Porto Corallo (south-east coast), these are all northern coastal localities. The species was never found during the period of ERLAAS operations, and only showed up again this past summer (1952) in a few isolated areas.

Corsican localities.—Padulone, near Cateraggio (Brumpt, 1925); east coast south to Solenzara and north coast to Calvi (Galliard & Sautet, 1934*a*, *b*,* 1935); numerous localities on east coast from Cap Corse to Solenzara (Jaujou & others, 1950); Porto Vecchio* (26.viii.52).

Anopheles marteri Senevet and Prunnelle 1927. Archives de l'Institut Pasteur d'Algérie, **5**, p. 529.

Unless the specimen is badly brushed, the pale apical wing fringe will differentiate *marteri* from the closely similar *claviger* and *plumbeus*. In addition, the apical segment of the female palpus is more than ½ as long as the pre-apical segment, the apices of the femora and tibiae are quite markedly pale scaled, and the first tarsal segment of the fore-leg is considerably longer than segments 2–5 combined. The male terminalia are distinctly characteristic.

The mature larvae are notable for the well-developed inner hair (1) of the submedian prothoracic group (shoulder hairs 1, 2, 3) and the palmate hair leaflets prolonged into pseudofilaments. As in *claviger*, there is a somewhat weakly developed, non-serrated palmate hair on the metathorax. ~~In addition, another character, which appears to be unique, is the short, spine-like hair (1) of the first abdominal segment (palmate hair of other segments)~~. First-instar larvae are most likely to be confused with those of *claviger* and *algeriensis*, from which they may be fairly readily separated by the length of the subantennal (11) and terminal antennal (4) hairs.

The pupae are unique for the fringe of long hairs practically encircling the paddles except for their bases. The prominent, curved terminal seta of the paddle is noteworthy, but this is also a characteristic of *hispaniola* and *superpictus*, in which species, however, it is markedly hooked.

I have not seen the eggs of *marteri*, so have relied on Hadjinicolaou's description (1938). The eggs most closely resemble those of *claviger*, from which they differ by the greater size of the floats and by their rough texture.

Breeding places.—Normally the larvae are found in mountain streams, either flowing or interrupted; cool, shaded waters are preferred.

Sardinian localities.—First encountered in 1946 during the ERLAAS project. Widely distributed, but most commonly found in the mountains of the south-eastern quarter of the island where the larvae are quite abundant in certain local situations; the species has been taken from sea level up to 1,000 metres.

Corsican localities.—Corte* (Langeron & Galliard, 1933). Widespread throughout the island from sea level to 1,000 metres, but has not been collected as extensively as in Sardinia; Pont de Vecchio, Matra, Pietra, Morosaglia, Col de Prato, Marinca (Jaujou & others, 1950); Solaro, Serra, Vescovato, Pinello (Jaujou & others, 1951).

Anopheles plumbeus Stephens 1828. The Zoological Journal, **3**, p. 503.

Adults of *plumbeus* are distinguished with difficulty from those of *claviger* and *marteri*. Edwards (1928) described the variety *corsicanus* based on its smaller size (female palpi $\frac{3}{4}$ length of proboscis, the last two segments together scarcely shorter than the preceding segment, and the hind tarsi (1–5) slightly over twice the length of the hind tibia); I have failed to notice any significant difference, however, from typical *plumbeus* in reared material from Mignattaja, Corsica. The palpi are as long as the proboscis; the last two segments are considerably shorter than the preceding palpal segment, and the hind tarsi are about 2·5 times as long as the tibia. I could find no difference either in the male terminalia, the larvae, pupae or eggs (the latter from Sardinia).

The larvae are easily identified by their dark appearance, large oval head with its reduced hairs and the conspicuous pinnately-branched lateral hairs on abdominal segments 1–6. Likewise there is no difficulty in recognising first-instar larvae by the very short, apically-branched subantennal hair (11) and the apically-branched clypeal hairs.

The pupa is unique among those of Anophelines occurring in the islands in having the lateral spine of the eighth segment long, slender and unbranched. The paddles have minute serrations along the external posterior border, but not reaching to the terminal hair.

The eggs are distinctive for their diamond-shaped appearance, absence of floats and conspicuous marginal frill.

Breeding places.—Ordinarily found in tree holes, but occasionally occurs in artificial containers, rock or ground depressions containing a rich infusion of fallen leaves.

Sardinian localities.—First found during the period of the ERLAAS project. Widely distributed in lowlands and mountains wherever trees with rot-holes occur.

Corsican localities.—Vico (Catanei, 1925); Porto (Edwards, 1928); Mignattaja* (17.v., 4.vi., 14.vi.44); Morosaglia (Jaujou & others, 1950).

Anopheles superpictus Grassi 1899. Atti della Reale Accademia dei Lincei. Rendiconti. 5th series, **8**, p. 560.

The adults of *superpictus* closely resemble those of *hispaniola*. Ordinarily the terminal segment of the palpus is entirely pale, but sometimes there is a dark central band and such individuals might be confused with some specimens of *hispaniola*. Additional characteristics are given under the latter species (see also Edwards, 1921, and Gil Collado, 1930).

The mature larva is readily separated from *hispaniola* by the characters given in the key. In addition, the terminal filaments of the palmate leaf elements are longer in *superpictus* and only one of the two mesothoracic pleural hairs (9, 10) is branched. Both species have palmate hairs on segments 2–7, those on the second segment having fewer elements. I have not seen any tiny branchlets on the inner clypeal hairs of Corsican specimens as reported for this species (Senevet, 1935). I do not know the first-instar larva but presume it to be similar to *hispaniola* (La Face, 1929).

The pupa resembles that of *hispaniola* in having a prominent, hooked terminal seta on the paddle, but the large teeth fringing the external posterior margin of the paddles have been replaced by long hairs. A few tiny hairs continue beyond the terminal seta along the internal margin for a short distance. The subterminal seta is short, much branched apically and is inserted farther away from the terminal seta, so that it does not reach the posterior margin of the paddle.

I have not seen the eggs of *superpictus* and have relied on the descriptions of Theodor (1925) and Bates (1941) for the characters used in the key; apparently it is readily distinguished. The exochorion of the ventral surface has no trace of a hexagonal pattern such as seen in *hispaniola*.

Breeding places.—Similar to those of *hispaniola*.

Sardinian localities.—Sardinian mountains (Missiroli, 1944). This is a dubious record as the species was never found in the thousands of collections made during the period of ERLAAS.

Corsican localities.—The only reference to this species that I can find is the following statement by Senevet (1935, p. 290): "La faible dispersion de l'*A. superpictus* en France, Corse et Afrique du Nord, ne justifierait pas une carte de distribution."; later (p. 303) Senevet does not include *superpictus* in his list of Corsican Anophelines. During 1944, I found the larvae and pupae of this species (from which one male was reared) in the Bravone river, Bravona (4, 18.ix.44); the collections also included the immatures of *labranchiae* and *Culex mimeticus* Noé. One female was taken in a house at Prunette (17.x.44). Both localities are on the east coast.

Genus URANOTAENIA.

Uranotaenia unguiculata Edwards 1913. Journal and Proceedings of the Asiatic Society of Bengal, (N.S.) **9,** p. 51.

The adults are small dark mosquitoes and, apart from the generic characters used in the key, are notable for the extremely tiny palpi in both sexes and a conspicuous band of broad, flat, bluish-white scales along the lateral margin of the mesonotum from the wing base to the head; a similar band also runs across the pleurae from the posterior pronotum to the mesepimeron. The mesonotum proper is clothed with tiny dark brown scales. The wing scales are dark, except for a short line of bluish-white scales at the base of the first vein. The abdominal tergites are essentially covered with dark brown iridescent scales, although there are traces of paler scales laterally. The legs are largely dark, with patches of bluish-white scales at the tips of the femora and tibiae, a stripe along the basal 2/3 of the anterior surface of the middle femora, and a short subapical stripe on the dorso-anterior aspect of the hind tibiae. The male terminalia are characterised by a short, conically-shaped basistyle, bearing several long, stout setae on the basal lobe. The dististyle is short, stout and expanded at the midpoint of the inner surface; the spine is subterminal in position and pointed.

The larvae are easily recognised by the characteristic sclerotised lateral plate of the eighth abdominal segment, from which 6–8 comb spines arise in a row along the posterior margin. The latter consist of a strong short tooth projected on a conspicuous triangular base which is bordered with fine hairs; the middle spines are the largest. The siphon is long and somewhat sigmoid-shaped, index about 4 : 1. The pecten is composed of about 18–20 *scales* which reach to the tuft, about midway along the siphon; the siphon tuft is 7- to 8-branched and about the same length or slightly longer than the siphon width at the tuft's point of origin. The anal saddle completely encircles the segment and carries a 4- to 5-branched saddle hair which is about the same length as the saddle; the posterior margin of the saddle is conspicuously spinose. The anal gills are pointed and generally shorter than the anal saddle. The head is dark and broadly oval, being slightly broader than long. The antennae are about 1/4 the length of the head, have a few minute spicules and a tiny single shaft hair inserted at about the midpoint. The middle and inner frontal hairs are stout and single, the latter being shorter, and in one instance 2-branched.

Breeding places.—Canals, ditches, and stream and marsh pools containing rich growths of horizontal vegetation; also found in densely shaded situations.

Sardinian localities.—Ischois, Assemini* (27.vii.52); and Corongiu, Quartu Sant'Elena* (14.viii.52).

Corsican localities.—Tavignano river and Debbie marsh, Cateraggio; Sale lagoon, Ghisonaccia (Galliard, 1927*a*); Ghisonaccia* (7.viii.44), Bravona* (4.ix.44), Sandali river, Alistro* (9.viii.44), and Tangicia pumping station, Poretta* (25.viii.52).

Genus CULISETA.

Key to species of *Culiseta*.

Larvae.

1. Antennae short, not more than half length of head; antennal tuft extending barely, if at all, beyond tip of antennae. Siphon short, index less than 4 : 1 2

   Antennae about as long as head; antennal tuft extending well beyond tip of antennae. Siphon more slender, index over 4 : 1 4

2. Head with mid and inner frontal hairs single. Anal saddle incomplete. Siphon index 2 : 1 or less; pecten composed of irregular row of about 12 spines (some not toothed) both on and off the siphon .... *longiareolata* (Macq.)

   Head with frontal hairs multiple. Saddle completely ringing anal segment. Siphon index between 3 and 4 : 1, pecten composed of about 30 elements, the apical ones long and hair-like, the basal ones toothed spines 3

3. Head with distance between post-clypeal hairs equal to, or greater than, distance between inner frontal hairs .... *annulata* (Schr.)

   Head with distance between post-clypeal hairs usually much less than distance between inner frontal hairs .... *subochrea* (Edw.)

4. Siphon with prominent, much-branched apico-dorsal hair tufts; pecten occupying much more than 1/2 length of siphon and terminating in 2–4 large, isolated, simple spines .... *fumipennis* (Steph.)

   Siphon with tiny, unbranched apico-dorsal hairs; pecten occupying much less than 1/2 length of siphon (terminal 1–2 spines may be isolated but are toothed) 5

5. Length of siphon tufts usually less than 2/5 that of siphon .... *morsitans* (Theo.)

Length of siphon tufts usually more than 2/5 that of siphon ... *litorea* (Shute).

Adults.

1. Thorax with rather sharply defined white lines. Femora and tibiae striped and spotted. Palpi of males shorter than proboscis ... *longiareolata* (Macq.)

Thorax without sharply defined lines. Femora and tibiae not striped. Palpi of males as long or longer than proboscis 2

2. Wings with scales clustered to form dark spots; cross-veins in nearly straight line. Tarsi with broad, conspicuous basal pale rings 3

Wings unspotted; cross-veins well separated. Tarsi with narrow, somewhat inconspicuous rings 4

3. Wing with 5th vein entirely dark scaled; spots distinct; cross-veins in line or posterior vein slightly toward wing base. Abdominal tergites having pale scales (largely white) restricted to basal bands ...... *annulata* (Schr.)

Wing with 5th vein having some pale scales; spots less distinct; cross-veins in line or (more usually) posterior vein shifted toward wing apex. Abdominal tergites having yellow scales scattered over dark areas ... *subochrea* (Edw.)

4. Proboscis of females uniformly dark (or with very few pale scales on middle 1/3). Abdominal sternites with diffused light and dark scales ...... *morsitans* (Theo.)

Proboscis of female with scattered pale scales, chiefly in middle 1/3. Abdominal sternites with dark scales forming inverted " V " patterns ... 5

5. Tarsi with pale rings conspicuous at all joints. Palpi of males with last segment extending at least 1/2 its length or more beyond tip of proboscis; 3rd and 4th segments densely setose .... *fumipennis* (Steph.)

Tarsi with pale rings less distinct at last two joints on fore- and mid-legs and inconspicuous or absent on hind legs. Palpi and proboscis of males approximately coequal; 3rd and 4th segments of palpi with few setae ...... *litorea* (Shute).

Males.

1. Ninth tergite lobes expanded into conspicuous, long, knobbed sclerotised processes, bearing tiny spine-like setae. Dististyles expanded apically and bluntly rounded; terminating in 2–3 short, pointed spines ... *longiareolata* (Macq.)

Ninth tergites with small membranous lobes bearing long setae. Dististyles tapering apically and terminating in single, blunt claw 2

2. Phallosome consisting of 2 long, slender, pointed sclerotised processes 3

Phallosome broad, consisting of 2 rounded, sheath-like membranous plates 4

3. Basistyles having basal lobes with 2 (rarely 3) setae conspicuously stouter than the rest. Eighth tergite lobe usually devoid of spines ...... *annulata* (Schr.)

Basistyles having basal lobes with 3–5 setae conspicuously stouter than the rest. Eighth tergite lobe usually with few scattered spines ...... *subochrea* (Edw.)

4. Basistyles not more than twice as long as basal width, bluntly tapered; basal lobes with 2 conspicuously stout setae, the longer reaching at least to tip of basistyles .... *litorea* (Shute)

Basistyles about 2·5 times as long as basal width, markedly tapered apically; basal lobes with 3 or 4 conspicuously stout setae, all terminating considerably short of tip of basistyles 5

5. Dististyles slender, width at centre about 1/16 of their length ... *fumipennis* (Steph.)

Dististyles stouter, width at centre about 1/12 of their length ...... *morsitans* (Theo.).

Culiseta annulata (Schrank) 1776. Beyträge zur Naturgeschichte. Fritsch, Leipzig, p. 97 (*Culex*).

This is one of the largest mosquitos in the islands, and the most common *Culiseta*. It is readily separated from all its relatives except *Culiseta subochrea* (Edw.) by its conspicuous black and white legs, with white pre-apical rings on the femora, white-tipped tibiae (not always distinct) and white basal rings on the first four tarsal segments; in addition, the first tarsal segment has a white band in the middle. The abdominal tergites are black, with somewhat narrow white basal bands; the second tergite carries a characteristic median white stripe. The wings are largely clothed with dark scales, which are clumped together to form spots at the base of the second vein, at the cross-veins, and at the base of the anterior and posterior fork cells; furthermore, the cross-veins form a straight line, or nearly so; some pale scales are present on the costa, subcosta and first vein. The colour characters of the wing and abdomen, just mentioned, should separate the species from *subochrea* in most cases.

The male terminalia are said to differ from *subochrea* in having two, rarely three (rather than 3–5) stout setae on the basal lobes of the basistyles, and by the usual absence of spines on the lobe of the eighth tergite (normally present in *subochrea*; Marshall, 1938). In 11 terminalia preparations of Sardinian material, six have two stout setae per lobe on the basal lobes and no spines on the eighth tergite lobe (*annulata*). In the remaining five, the basal lobe setae vary from two to three in the same specimen (both lobes with three setae in one case), and four of these preparations have one or two spines on the eighth tergite lobe; the fifth has no spines. At least four of these terminalia might conceivably refer to *subochrea*, but the variation is such that they could belong to either species; unfortunately the adults are in such poor shape that they are of no help. Both *annulata* and *subochrea* are said to have more or less distinct hairy subapical knobs on the basistyles, but they are not at all clear in the present preparations.

The larvae of *annulata*, together with those of *subochrea* and *longiareolata*, are characterised by short antennae and antennal shaft tufts and stout air tubes. The former two species, *annulata* and *subochrea*, are similar in having the distal elements of the pecten hair-like rather than in the form of spines, as are the basal elements. According to Marshall, these two may be separated with some degree of success by the distance between the post-clypeal hairs being equal to, or greater than, the distance between the inner frontal hairs in *annulata*; in *subochrea* the post-clypeal hairs are much closer together. Unfortunately, however, this character also is subject to considerable variation and will not always suffice to determine the individual larva. The siphon index is between 3 and 4:1. The mid-frontal hairs are normally 3-branched, with the central branch stout, and the inner frontal tufts vary from 6–9 branches. The antennal shaft tufts have about 15 branches.

Breeding places.—The species breeds in a wide variety of habitats, including seepages, ground pools, water troughs, ditches, etc. Marshall reports it also from brackish water, tolerating salinities up to 35 per cent. sea water. The writer once found it in a tree hole in Corsica.

Sardinian localities.—Originally reported from the island by Ficalbi (1899) as *Culex annulatus* Schr. The species is widespread and common.

Corsican localities.—Fairly common throughout the island, coastal regions and mountains: Vizzavona (Galliard, 1927*a*); Ajaccio * (1.iii.44), Alesan swamp, Alistro * (19.v.44), Mignattaja * (19.v.44), Prunelli * (19.v.44), Trinité * (22.v.44) and Ghisonaccia * (7.viii.44); Lumio, Calvi * (20.iii.52, Casalta), Lozari, I'lle Rousse * (21.iii.52, Casalta) and Argentella Mina, Calvi * (21.iii.52, Casalta).

Culiseta fumipennis (Stephens) 1825. The Zoological Journal, **1**, p. 453 (*Culex*).

The largest mosquito in the islands, *fumipennis* is a brown species with unspotted wings and black abdomen having narrow transverse bands of pale scales. The legs are largely dark with tiny pale spots at the femoro-tibial and tibio-tarsal joints and narrow pale rings on all tarsal segments, which are essentially basal but which do overlap very slightly on to the preceding segments. The abdominal sternites are characterised by black inverted " V " patterns on a pale background. The proboscis of both sexes is clothed with an admixture of pale and dark scales. The palpi in the male are distinctly longer than the proboscis, by at least half the length of the terminal segment or more; contrary to Marshall's findings (1938) in English specimens, however, the junction of the last two segments is coequal with the labio-labellar division or falls short of this mark (three specimens from Orune, Sardinia). Taking the length of the labium as 100, the combined length of the first four segments varies from 94·7 to 100, rather than from 102·5 to 106 as reported by Marshall. The length of the first tarsal segment of the fore-leg in the three male specimens before me equals the combined length of the remaining four segments. Two slide preparations of the male terminalia agree closely with published descriptions, and are readily identified by the characters indicated in the key.

Like the adult, the larvae of *fumipennis* are large. Their air tubes are fairly long and slender, index about 4·5 : 1, and are notable for the long pecten which occupies 50–70 per cent. of the length of the siphon, and for the more distal spines which are very large, isolated and simple. In addition, there is a pair of conspicuous apico-dorsal setal tufts (2) which have a robust base and are much branched; the ventral valves are adorned with two prominent setae (9) which are hooked rather than sinuous.

Breeding places.—The larvae may be found in open situations, in temporary pools, or the weedy margins of permanent ones (Marshall).

Sardinian localities.—Present information seems to indicate this to be a mountain species. Caserma Sant'Efisio, Orune* (3.iii.47), Orune* (9.v.47), Tandalo region, Budduso* (12.iii.48) and Alá dei Sardi* (11.iii.48).

Corsican localities.—None.

Culiseta litorea (Shute) 1928. The Entomologist, **61**, p. 186 (*Culicella morsitans* var. *litorea*).

Adults of this species are easily confused with *fumipennis*, and to a lesser extent with *morsitans*. In the two male specimens before me, the inverted " V " patterns on the abdominal sternites are distinct and the tarsal rings are very inconspicuous. The most notable point is the length of the palpi which are approximately the same length as the proboscis; they are longer in both *fumipennis* and *morsitans*. The length of the first tarsal segment of the fore-leg is slightly longer than the combined length of the remaining four segments. The male terminalia are very distinctive and permit the only reliable means of separating *litorea* from its close relatives. Two slide preparations agree very closely with the description published by Marshall and Staley (1933). The ratios of the length of the basistyle to its basal width are 2·09 : 1 and 1·8 : 1. The apices of the basistyles are blunt. The basal lobes have two stout setae, one of which extends beyond the apex of the basistyle. The ratios of the central width of the dististyle to its length are 0·045 : 1 and 0·033 : 1. The ratios of the length of the dististyle to the length of the basistyle are 0·83 : 1 and 0·91 : 1, and the number of teeth of the tenth sternites (paraprocts) varies from 2 to 3 on both specimens.

The larvae are readily distinguished from those of *fumipennis*, but the separation from *morsitans* is much less secure. The siphon tufts are said to be longer in *litorea* (Marshall, 1938), being more than 2/5 the length of the siphon; however, the extremes of variation in the two species overlap each other. Three larvae from the same locality as one of the males (Piscina Rodas, Alghero) have siphon tuft ratios of 0·37 : 1, 0·37 : 1 and 0·40 : 1. These are borderline figures which could represent either species. Because of the collection of the male at the same time, these larvae are ascribed with some hesitation to *litorea*. The siphon index is about 6 : 1; the pecten occupies about 25 per cent. of the siphon, and the apical 1–2 spines may be isolated somewhat but they are usually toothed. The terminal setae (9) of the ventral valves are prominent and sinuous rather than hooked. The middle and inner frontal head hairs are 2- to 3-branched.

Breeding places.—The larvae are said to breed in coastal marshes, and are able to tolerate brackish water up to 15 per cent. sea water (Shute, 1928; Marshall, 1938). The breeding place of the above larvae was a large coastal fresh-water marsh, containing abundant growths of cat-tails.

Sardinian localities.—Tenuta Minola, Uta (male, 24.iii.47) and Piscina Rodas, Alghero (male and larvae, 20.iii.48). These are believed to be the first records of the species outside of England; both are coastal localities, one in the north-western part of the island and the other in the south.

Corsican localities.—None.

Culiseta longiareolata (Macquart) 1838. Diptères Exotiques Nouveaux ou Peu Connus. Librarie de Roret, Paris, **1**, (1), p. 34 (*Culex*).

An easily recognised species, *longiareolata* may be immediately identified by its pale appearance, due to the predominance of white scales on the head and palpi which form lines on the mesonotum and legs as well as patches on the pleurae; otherwise the scaling is light brown or yellow (rarely blackish). The wings are clothed with dark scales, except for a line of white ones along the anterior surface of the costal vein; clumping of the scales at the base of the second vein, the cross-veins and the base of the fork of the fifth vein gives the appearance of spotting. The cross-veins are well separated. The abdominal tergites have white basal bands and otherwise are clothed with yellow scales, but with some admixture of black. The legs are noteworthy for the fairly distinct pre-apical ring on the femora, the longitudinal streak of white scales on the femora, tibiae and first tarsal segment, and the basal bands on the first three tarsal segments. The male terminalia are characteristic for the conspicuous ninth tergite, which is expanded into two shiny sclerotised lobes, readily seen with a hand lens on unmounted specimens.

The larvae have a short, somewhat conically-shaped air tube, index about 1·5 : 1, on which there is an irregular row of short pecten spines occupying at least 75 per cent. of the siphon and extending anteriorly on to the membrane; the more apical spines are large and simple. Both the middle and inner frontal hairs of the head are simple. The antennal shaft tufts are usually 2-branched.

Breeding places.—The species has been found breeding in pools, tanks, wells, barrels and rock holes.

Sardinian localities.—Ficalbi first reported the species from Sardinia in 1899 as *Culex spathipalpis* Rond. While not particularly common, *longiareolata* is widespread throughout the island, at least in the lowlands.

Corsican localities.—Casabianda (Galliard, 1927*a*); Ajaccio * (5.iii.44) and Prunette * (28.vii.44).

Culiseta morsitans (Theobald) 1901. A Monograph of the Culicidae or Mosquitoes. The British Museum (Natural History), London, **2**, p. 8 (*Culex*).

The adults are very similar to those of *fumipennis* and *litorea*, but may be recognised fairly readily by the usually black proboscis and absence of dark inverted " V " patterns on the abdominal sternites. The wings have dark scales only and are unspotted; the cross-veins are widely separated. According to Marshall (1938), the last two tarsal segments are entirely dark. In the few poor specimens available for study (females only), I find that none of the tarsal rings are at all conspicuous. The male palpi are said to be distinctly longer than the proboscis and the joint of the last two segments overlaps the tip of the proboscis. Distinctive characters of the male terminalia are summarised in the key.

The larvae are very similar to those of *litorea*, but are said to differ by having shorter siphon tufts, these usually being less than 2/5 the length of the siphon (Marshall). I have seen no larvae from the islands definitely referring to this species.

Breeding places.—The larvae are reported as being found in aquatic situations similar to those of *litorea*, also ground depressions and pools (Marshall).

Sardinian localities.—Cabras (22.x., 2.xi.48), Castello Medusa, Tortoli (30.xii.48).

Corsican localities.—Padulone (Galliard, 1927*a*); Borgo (Edwards, 1928).

Culiseta subochrea (Edwards) 1921. *In* Wesenberg-Lund, Det Kongelige Danske Videnskabernes Selskabs Skrifter. Naturvidenskabelig og Mathematisk Afdeling. Copenhagen, 8th series, **7**, p. 198 (*Theobaldia annulata* var. *subochrea*).

I originally overlooked *subochrea* in compiling this review, but a single female from Tortoli, Sardinia, previously considered to be an abnormally-scaled *annulata*, seems to fit the description of *subochrea*. The cross-veins in one wing are in line and in the other, the posterior vein is slightly in advance (*i.e.*, toward the apex of the wing). The wing is less distinctly spotted, and there is an admixture of pale and dark scales on the fifth vein in addition to the costa, subcosta and first vein. The abdominal tergites have a scattering of yellow scales in the dark areas which gives a speckled effect. Moreover, the legs are more speckled than those of *annulata* due to a greater number of white scales scattered on the femora, tibiae and first tarsal segments. The characteristics of the male terminalia have been discussed under *annulata*.

The larval characters distinguishing *subochrea* from *annulata* have also been discussed under the latter species. In a collection of three larvae from Ghisonaccia, Corsica, two have the appearance of *subochrea*, as the post-clypeal head hairs are quite close together. Taking the distance between the inner frontal hairs as 100, the index figures for the distance between the post-clypeal hairs are 77 and 85 for these two larvae as compared with 116 for the third. Two pupae, however, in the same collection are *annulata*, as the minute denticles fringing the paddles are blunt rather than pointed as in *subochrea*.

Breeding places.—Similar to those of *annulata*—ditches, ponds, garden and farmyard tanks, etc., fresh and brackish water (Marshall, 1938).

Sardinian localities.—Tortoli (30.xii.48).

Corsican localities.—Ghisonaccia * (4.ix.44).

Genus ORTHOPODOMYIA.

Orthopodomyia pulchripalpis (Rondani) 1872. Bullettino della Società Entomologica Italiana, **4**, p. 31 (*Culex*).

As only larval material is available, the description of the adult is taken from Marshall (1938). This is one of the most elegant species in the islands. Against a black background, white scales form a conspicuous pattern, details of which include: apically- and basally-banded hind tarsi (last segment entirely white), basally-banded abdominal tergites, six-striped mesonotum, and banded palpi and proboscis. The wing scales are dark except for a short line of white scales at the base of the subcosta and first vein. The palpi of the female are notable for their length, being about half as long as the proboscis. In addition, the fourth tarsal segment of the fore-leg in both sexes is no longer than broad. The male terminalia are characterised by having the spine of the dististyle divided into five " fingers ", one of which is stouter than the rest. The basal lobe of the basistyle carries four stout spine-like setae. Claspettes are absent.

The larvae are distinctive for the absence of a pecten on the siphon and the presence (in the fourth instar) of sclerotised plates on the dorsum of abdominal segments seven and eight, and sometimes on the apical portion of six; there is also a narrow lateral plate on the anal segment at the base of the saddle. The comb of the eighth segment consists of two more or less superimposed rows of 23–30 *spines* and *scales*, the former being found in the middle; the posterior row has the longest spines. The siphon is black and slender, index about 4 : 1; the tuft consists of about 12 long branches (about 2/3 as long as the siphon) and is inserted at the basal 2/5. The anal gills are unequal in size, the longer dorsal pair being shorter than the saddle which completely rings the anal segment. The head is black, oval and slightly longer than wide. The antennae are short, less than 1/4 the length of the head, devoid of spicules and constricted beyond the middle; the shaft tuft is inserted at about 1/3, is 3- to 6-branched and slightly over 1/3 the length of the antenna. The frontal head hairs and post-clypeals are much-branched and conspicuous, mid-frontals 9- to 10-branched, inner frontals 7- to 8-branched and post-clypeals 5- to 7-branched. The general coloration of the larva is pinkish.

Breeding places.—Tree holes.

Sardinian localities.—Gadoni * (9.ix.48), Budduso * (22.ix.48) and Alà dei Sardi * (25.ix.48).

Corsican localities.—None.

Genus TAENIORHYNCHUS.

Taeniorhynchus buxtoni Edwards 1923. Bulletin of Entomological Research, **14**, p. 9.

The adults of *buxtoni* are readily separated from those of *richiardii* by the following characters. The scales of the proboscis and palpi are uniformly blackish-brown, and those of the mesonotum golden brown but paler around the wing bases and antescutellar space. The wing scales are uniformly dark and, while conspicuous, are not as broad as in *richiardii*. The legs are generally dark with a purplish hue when viewed from above; below, they are ochreous. The femora and tibiae have pale tips and the tarsi are unbanded. The abdomen is largely clothed with dark scales having a purplish gloss, but with whitish scales confined to the latero-basal angles of the tergites; the sternites have pale basal bands.

As the opposite sex has not previously been known, the terminalia of a Sardinian male are herewith described (the specimen to be deposited in the British Museum). The basistyle is 1·6 times as long as broad. The basal lobe is heavily sclerotised and bears apically a stout blunt rod, which is about 9·5 times as long as wide; at the apex of the rod are fine striations. Arising alongside of the rod is a slender shorter seta (this seta is also present in *richiardii* but has previously escaped notice). The dististyle is shorter than the basistyle by about $\frac{1}{4}$ and shaped not unlike the stinger of a scorpion (fig. 2). Beyond the slightly expanded base, the central portion is stem-like for a short distance and then expanded inwardly at right angles into a bulbous structure which terminates in a sinuous point bearing a short slightly curved spine; four delicate setae are inserted before the spine on the outer margin. The phallosome bears tiny denticles along the inner membranous edge. The tenth sternites (paraprocts) are heavily sclerotised apically and provided with 5–6 teeth. The lobes of the ninth tergites are adorned with 4–5 short, weak setae. The eighth tergite has a median patch of 9 stout setae on the apical margin.

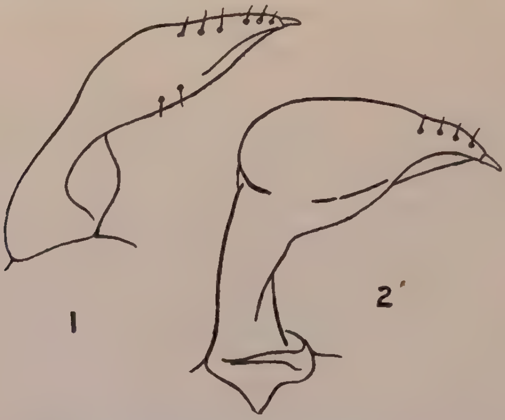


Fig. 2.—Dististyles of the male terminalia of (1) *Taeniorhynchus richiardii* and (2) *T. buxtoni.*

The terminalia of *buxtoni* are very similar to those of *richiardii*. The principal difference lies in the shape of the dististyle, which in the latter is basally broad, contracted and twisted in the middle, and then apically expanded into a long attenuated process; there is no stem-like base which expands into the bulbous structure typical of *buxtoni*. Characters of lesser importance typifying *richiardii* include the more rounded basistyles which are 1·45 times as long as wide, the greater number of tiny setae on the dististyle, as well as the greater number of setae on the lobes of the eighth and ninth tergites, those of the latter being more robust in *richiardii*.

The palpi of the male are longer than the proboscis by the length of the last segment.

The larvae are unknown.

Breeding places.—Presumably the larvae are found in situations comparable to those associated with *richiardii*. A large marsh known as Mare Foghe was probably the source of the Sardinian adults.

Sardinian localities.—San Vero Milis, two females and one male (12, 13.viii.48).

Corsican localities.—Stables at Padulone (Galliard, 1928); Ghisonaccia, two females biting in the woods (7.viii.44).

Taeniorhynchus richiardii (Ficalbi) 1889. Bullettino della Società Entomologica Italiana, **21**, p. 50 (*Culex*).

This species is not included in my material from the islands, hence the description of the adult is based on a male from Letchworth, Hertfordshire, England (June 1918, F. W. Edwards), kindly provided by Mr. P. F. Mattingly of the British Museum. The proboscis is essentially pale scaled except for the apex; likewise the palpi, which have the dark scales largely restricted to the apices of the terminal three segments. The mesonotum is clothed with silvery-grey scales. The wings and legs are speckled with broad light and dark scales. The tarsi have a pale basal band on all segments and, in addition, the first segment has a central ring. The abdominal tergites are clothed with dark brown scales but with pale ones forming basal lateral patches which tend to fuse medianly; some pale scales are also scattered amongst the brown; the sternites are pale scaled. The male terminalia are characterised by a conspicuously sclerotised basal lobe bearing a stout rod. There are no claspettes. The dististyle is strongly twisted and apically expanded and pointed; near the apex on the outer margin are 6–7 tiny setae, and two more are located further posteriorly on the inner margin (fig. 2). The lobes of the ninth tergite each bear about eight fairly strong setae, and the eighth tergite has a median clump of 17 setae on the apical margin.

The larvae of *Taeniorhynchus* are unique in having the air tube modified with toothed structures for piercing plant tissues; it bears no pecten. The comb of the eighth abdominal segment consists of about 15–24 *spines* in a somewhat irregular row. The anal saddle is long and encircles the segment; the saddle hair is 3-branched and inserted well forward of the posterior margin of the saddle. The gills are equal and shorter than the saddle. Both upper (2) and lower (3) caudal hairs are much-branched. The antennae are very long, longer than the head, and the portion distal to the shaft tuft is much more slender and about twice as long as the basal portion (Marshall, 1938).

Breeding places.—The larvae attach themselves to the roots and submerged stems of aquatic plants, presumably in more or less permanent bodies of water. Marshall lists the following plant " hosts ": *Ranunculus*, *Acorus*, *Glyceria*, *Typha* and *Hydrocharis morsus-ranac*, the latter a species used by Galliard in the laboratory.

Sardinian localities.—Platamona lagoon, Portotorres *? (Some larvae collected by Mr. Garret Jones in the summer of 1948 were tentatively identified by me as belonging to this species. This was before the existence of *buxtoni* in Sardinia was known. Unfortunately these larvae have been lost.)

Corsican localities.—Padulone, near Cateraggio (Brumpt, 1925); mouth of Tavignano river, Cateraggio and further north at Giustiniana (Galliard, 1927*a*).

Genus AËDES.

Key to species of *Aëdes*.

Larvae.

1. Antennae without spines 2

Antennae with spines. (Note: very few spines in *longitubus*, but long siphon is characteristic) 4

2. Antennal tuft 2- to 3-branched. Siphon tuft inserted at about 2/3 length of siphon and within the pecten, the last spine of which is isolated ... *vittatus* (Big.)

Antennal tuft a single hair. Siphon having pecten and tuft otherwise 3

3. Siphon with pecten terminating considerably short of hair tuft, which is inserted before the middle. Abdominal tergites adorned with many stellate hair tufts .... *geniculatus* (Ol.)

Siphon with pecten terminating at hair tuft, which arises just beyond the middle. Abdominal tergites without conspicuous stellate hair tufts ...... *aegypti* (L.)

4. Siphon with 3–4 pairs of single setae on dorsal surface; two pairs of hair tufts arising within pecten, the latter having isolated teeth apically. Anal gills shorter than saddle .... *rusticus* (Rossi)

Siphon otherwise 5

5. Siphon with pecten having apical spines isolated; hair tuft very small and situated well beyond middle of siphon and beyond the pecten. Anal gills long and tapering (about as long as siphon in *cinereus*) 6

Siphon having pecten without isolated spines apically; hair tuft variably placed but always large 7

6. Head with frontal and post-clypeal hairs arising almost in a straight line. Siphon more slender, index about 3:1 .... *cinereus* Mg.

Head with inner frontal hairs out of line in relation to others. Siphon stouter, index about 2:1 .... *vexans* (Mg.)

7. Anal gills usually rounded and much shorter than saddle (rarely exceeding 2/3 saddle length) 8

Anal gills about as long or longer than saddle, usually lanceolate 10

8. Siphon with hair tuft inserted midway of its length. Head with middle and inner frontal hairs having 2 or more branches .... *detritus* (Hal.)

Siphon with hair tuft inserted clearly beyond midpoint. Head with middle and inner frontal hairs single 9

9. Siphon tuft long, extending to or beyond apex of siphon from tuft's point of origin; spicules at apex of siphon conspicuous. Anal segment with upper caudal tufts longer than siphon .... *mariae* (Ed. & Et. Serg.)

Siphon tuft short, not reaching apex of siphon; spicules at apex of siphon inconspicuous. Anal segment with upper caudal tufts shorter than siphon .... *caspius* (Pall.)

10. Siphon long and slender, index 6·5:1 or more, black. Anal gills rounded, dorsal pair longer. Post-clypeal head hairs large and much branched ...... *longitubus* Cambournac

Siphon short and robust, index about 3 : 1 or less. Anal gills lanceolate and subequal. Post-clypeal head hairs small and inconspicuous 11

11. Head with middle and inner frontal hairs single. Abdominal segment 8 having comb composed of about 70–80 blunt-ended scales ...... *communis* (Deg.)

Head with middle and inner frontal hairs 2-branched or more. Abdominal segment 8 having comb composed of about 28–38 pointed spines .... *cantans* (Mg.).

Adults.

1. Tarsi dark 2

Tarsi with pale rings on some segments 6

2. Mesonotum clothed with yellowish-white scales except for 4 sharply-defined, longitudinal black lines, the lateral pair short. Legs with conspicuous knee spots .... *geniculatus* (Ol.)

Mesonotum otherwise. Legs with knee spots less prominent or absent ... 3

3. Mesonotum reddish-brown scaled, without ornamentation. Abdomen completely dark except for narrow lateral pale stripes. Palpi of males 1/3 length of proboscis or less .... *cinereus* Mg.

Mesonotum otherwise. Abdominal tergites with pale basal bands (some apical scaling in *rusticus*). Palpi of males longer than proboscis 4

4. Thorax with posterior pronotum having all scales flat and straight, the upper ones dark. Palpi of females 1/4 to 1/3 length of proboscis ... *rusticus* (Rossi)

Thorax with posterior pronotum having upper scales narrow and curved, all ochreous. Palpi of females less than 1/4 length of proboscis 5

5. Femora of front and middle legs conspicuously mottled in front with dark and light scales. Abdominal tergites usually with scattered pale scales in the dark parts .... *detritus* (Hal.)

Femora of front and middle legs with only a few pale scales in front. Abdominal tergites without pale scales scattered in the dark parts .... *communis* (Deg.)

6. Tarsi with both basal and apical rings on some segments 7

Tarsi with basal rings only on some segments 9

7. Abdominal tergites with pale median stripe in addition to transverse bands; sometimes almost entirely pale .... *caspius* (Pall.)

Abdominal tergites with basal bands only, no median stripe 8

8. Wings and legs densely speckled with light and dark scales. Tarsal segment 5 of *hind* legs only, entirely pale .... *mariae* (Ed. & Et. Serg.)

Wings and legs only very slightly, if at all, speckled. Tarsal segment 5 of *all* legs entirely pale .... *longitubus* Cambournac

9. Tarsal rings extremely narrow. Abdominal tergites with pale bands indented medianly. Mesonotum uniformly coppery-brown. Wing scales dark except for tiny patch at base of costa .... *vexans* (Mg.)

Tarsal rings broader, more conspicuous. Abdominal tergites with pale bands not indented 10

10. Body with pale scales generally yellowish-white, not silvery. Mesonotum generally dark brown. Hind leg with 5th tarsal segment black apically. Wing scales bicoloured .... *cantans* (Mg.)

Body with some pale scales metallic silvery-white. Mesonotum with distinctive ornamentation. Hind leg with 5th tarsal segment entirely white. Wing scales dark 11

11. Femora and tibiae not ringed. Mesonotum with white lyre-shaped design ... *aegypti* (L.)

Femora and tibiae with subterminal white rings. Mesonotum dark with 6 conspicuous white spots .... *vittatus* (Big.).

Males.

1. Dististyle unequally divided into 2 arms, arising before apex of basistyle ...... *cinereus* Mg.

Dististyle not divided, arising at apex of basistyle 2

2. Dististyle with subapical spine 3

Dististyle with apical spine 4

3. Dististyle expanded gradually to apex; subapical spine straight ...... *vexans* (Mg.)

Dististyle greatly expanded apically into conspicuous rounded knob; subapical spine curved strongly .... *vittatus* (Big.)

4. Claspettes absent. Basistyle with plaque bearing short erect spines .... *aegypti* (L.)

Claspettes present. Basistyle without such a plaque of spines 5

5. Basistyle having neither basal nor subapical lobes; no conspicuously different setae basally. Claspette stem much longer than appendage ... *geniculatus* (Ol.)

Basistyle usually having conspicuous basal and subapical lobes, the former usually with differentiated setae (subapical lobe inconspicuous in *longitubus* and *mariae*) 6

6. Basistyle with basal lobe bearing row of flattened setae. Dististyle having wavy terminal spine .... *rusticus* (Rossi)

Basistyle otherwise. Dististyle having straight or slightly curved terminal spine 7

7. Basistyle having small basal lobe, subapical lobe barely distinguishable 8

Basistyle having conspicuous basal and more prominent apical lobe 9

8. Basistyle with basal lobe having one very long apically-curved seta distinctly stouter and darker than remainder. Claspette appendage 1/4 longer than stem .... *longitubus* Cambournac

Basistyle with basal lobe having no differentiated setae. Claspette stem and appendage subequal in length .... *mariae* (Ed. & Et. Serg.)

9. Basistyle with basal lobe having at least 2 stout setae, one of which is markedly recurved .... *caspius* (Pall.)

Basistyle with basal lobe having only one conspicuous seta 10

10. Claspette having appendage as long as, or longer than, stem ... *detritus* (Hal.)

Claspette having appendage shorter than stem 11

11. Claspette having stem very long and curved; appendage long and narrow ... *communis* (Deg.)

Claspette having stem shorter and straight; appendage short and broad ...... *cantans* (Mg.).

Aëdes aegypti (L.) 1762. D. F. Hasselquists . . . Reise nach Palästina in den Jahren 1749 bis 1752. Auf Befehl Ihro Majestät der Königinn von Schweden herausgegeben von Carl Linnäus. Aus dem Schwedischen (von T. G. Gadenbusch). J. C. Koppe, Rostock, p. 470 (*Culex*).

I have not seen specimens of this ornate species from the islands, and as far as I am aware it has not been taken here in recent years. It is distinctive because of its clear-cut black and white appearance. The pale scales (some of which are broad and silvery-white) form a lyre-shaped pattern on the mesonotum, narrow basal bands on the abdominal tergites which are not joined to the lateral spots, and conspicuous basal rings on the tarsal segments, as follows: fore- and mid-legs (first two segments) and hind legs (first four segments); the fifth tarsal segment of the hind leg is usually entirely white. The wing scales are all dark, except for a tiny white spot at the base of the costa. The male terminalia have the phallosome divided into two lateral plates, each bearing teeth externally. The basistyle has no subapical lobe and the basal plaque, which covers most of the inner surface of the basistyle, is adorned with short erect spines. The dististyles are somewhat expanded in the middle (Edwards, 1941).

The larvae may be recognised by the following characters: non-spinose antennae; the antennal shaft hair as well as the frontal hairs of the head single; the comb of the eighth segment consisting of a single row of 7–12 *spines*; the pecten extending to the siphon tuft, which is situated beyond the middle; and the large sausage-shaped gills which are subequal and more than twice the length of the anal saddle (Hopkins, 1936).

Breeding places.—This species is usually found breeding in artificial containers.

Sardinian records.—Sardinia, as *Culex elegans* Ficalbi (Ficalbi, 1899).

Corsican records.—Bastia, as *Aëdes argenteus* (Poiret) (Langeron, 1925; Galliard,* 1928).

Aëdes cantans (Meigen) 1818. Systematische Beschreibung der Bekannten Europäischen Zweiflügeligen Insekten. F. W. Forstmann, Aachen, **1**, p. 6 (*Culex*).

I have not seen adults of this species from the islands. It is apt to be confused only with *Aëdes vexans* (Mg.), from which it differs in several respects. The basal rings of the tarsi are wider and they are found on all segments except the fifth of the fore-leg. The pale bands of the abdominal tergites are not constricted medianly, and they are both apical as well as basal on the more distal segments. The wing scales are bicoloured, and the mesonotum, while generally being dark brown, may have some pale scales clothing the sides of the middle third. The male terminalia are distinctive for the fairly long-stemmed claspettes with their broad flag-like appendage; the basal lobe of the basistyle bears a long stout seta as well as many smaller setae, and, in addition, a ventrally directed extension covered with hairs (Marshall, 1938).

The larvae should be readily identified by the characters indicated in the key. If, however, the anal gills have been lost or damaged, the species may be confused with *detritus*. It can be differentiated from the latter by the number of elements forming the comb of the eighth segment. According to Marshall, there are 45–65 comb *scales* (these being bluntly ended) in *detritus* whereas there are 28–38 *spines* in *cantans*, each with the central tooth stouter than the rest.

Breeding places.—These are said to be temporary pools in woodland areas. The writer collected some immature larvae thought to refer to this species from a reed swamp, the water having appeared as the result of a high tide in the nearby river (Corsica). This is a one-generation species.

Sardinian localities.—None.

Corsican localities.—Ghisonaccia and Porto Vecchio (Galliard, 1927*a*); Figarella river, Calvi * (24.viii.52).

Aëdes caspius (Pallas) 1771. Reise durch Verschiedene Provinzen des Russischen Reichs. Kayserlichen Academie der Wissenschaften, St. Petersburg, **1**, p. 475 (*Culex*).

Adults of this species are apt to be confused only with those of *mariae*, and possibly *longitubus*, as all three have some of the tarsal segments ringed at both extremities. The median yellow stripe of the abdominal tergites is ordinarily sufficient to distinguish *caspius*, but this may be faint or absent in an occasional specimen. In such instances, *caspius* may be separated from both species by the following: the dark scales of the legs and abdomen are brown rather than black; the abdominal tergites have basal bands of yellow scales and separate lateral patches of white scales; also, the mesonotum is covered with fawn-coloured scales, broken by two prominent pale stripes. The speckled wings, legs and proboscis are additional characters separating *caspius* from *longitubus*. The principal points distinguishing the male terminalia are indicated in the key.

Again, the larvae are likely to be confused with those of *mariae* (providing the breeding place is not known). In addition to the key characters, mention should be made of the siphon, which is narrower at the apex than at the base; in *mariae*, the apex and base are more nearly the same width. The siphon index is about 2·6 : 1, and the comb consists of 18–28 scales; the latter have the median tooth (and sometimes the submedian teeth) somewhat longer and stouter than the others, giving the scale a pointed appearance. The number of comb scales and their shape are of diagnostic value in differentiating *caspius* larvae from those of *detritus*.

Breeding places.—This is essentially a salt-marsh mosquito, fresh broods appearing subsequent to high tides, but the species may be found in fresh-water areas where periodic irrigation is practised. Larvae have been found in Sardinia in water with a salt concentration of 25 parts per thousand.

Sardinian localities.—Sardinia, (Cagliari) as *Culex penicillaris* Rond. (Ficalbi, 1899). Numerous localities along the coast where brackish-water marshes exist. Very troublesome in Cagliari at certain seasons both in the open and in houses. Found in the Arborea Bonifica, breeding in ditches, pastures and rice fields. Adult females have been taken near certain mountain communities (Villanova Tulo and Seui) where there was no possibility of their having been bred locally; the nearest breeding grounds down the Flumendosa river to the coast are 60–75 kilometres distant.

Corsican localities.—Abundant in July and August on the east coast, particularly at Padulone (Galliard, 1927*a*); south of Biguglia (Edwards, 1928); Porto Vecchio (22.v.44), Cateraggio * and Prunette (23.viii.44), Mignattaja * (12.ix.44).

Aëdes cinereus Meigen 1818. Systematische Beschreibung der Bekannten Europäischen Zweiflügeligen Insekten. F. W. Forstmann, Aachen, **1**, p. 13.

I do not have this mosquito in the material before me. It is a somewhat sombre-looking species with a reddish mesonotum (darker in males). The pale lateral stripes on the abdomen are very narrow and hardly visible from above.

The males are distinctive for their extremely short palpi and terminalia having a divided dististyle.

The larvae are notable for their long, tapering anal gills which are about the length of the siphon. The length of the siphon hair tuft is considerably shorter than the width of the siphon at the tuft's point of origin (Edwards, 1921; Marshall, 1938).

Breeding places.—This is a single-generation species. The eggs are laid in low-lying areas which periodically fill with water, such as river swamps, flooded pastures and shallow woodland pools (Marshall).

Sardinian localities.—None.

Corsican localities.—Ghisonaccia and Porto Vecchio (Galliard, 1927*a*).

Aëdes communis (De Geer) 1776. Mémoires pour Servir à l'Histoire des Insectes. P. Hesselberg, Stockholm, **6**, p. 316 (*Culex*).

I have not seen this essentially northern species in the islands. As a member of the dark-legged group of *Aëdes*, it may be distinguished from *geniculatus*, *cinereus* and *rusticus* by its pale basal abdominal bands of uniform width, and from *detritus* by the absence of pale scales scattered through the dark portions of the abdominal tergites. Difficulty may sometimes be encountered should the latter species have the pale abdominal scales limited to the basal bands, as sometimes occurs; in such instances, the absence of intense speckling on the front and middle femora will assist in the differentiation. The wing scales are dark. The general coloration of the mesonotum is dark brown. The male terminalia are characterised by having distinct subapical and basal lobes (the latter bearing only one stout, conspicuous seta) and claspettes with very long, curved stems; the appendage of the claspette is long and narrow and has two ridges at its base.

Some trouble might be experienced in identifying larvae which have lost or damaged anal gills. Those of *communis* will be recognised by the large number of blunt *scales* (70–80) composing the comb of the eighth abdominal segment, and the single middle and inner frontal hairs of the head (Marshall, 1938).

Breeding places.—The species is single brooded and the larvae are found in temporary collections of water in woodland areas.

Sardinian localities.—None.

Corsican localities.—Ghisonaccia and Porto Vecchio (Galliard, 1927*a*).

Aëdes detritus (Haliday) 1833. The Entomological Magazine, **1**, p. 151 (*Culex*).

Normally the adults of *detritus* are conspicuously speckled on the abdominal tergites, wings and legs, and as such are not to be confused with other local species. Occasional Sardinian specimens do not have speckled abdomens, and the pale scaling of the wings is so reduced that the species might be mistaken for *Aëdes punctor* (Kirby) or *communis*, as previously noted. The former, which is not known from the islands, is distinguished by the medianly-constricted, pale abdominal bands which take on a distinct inverted V-shaped appearance on the more distal tergites; in *detritus*, the bands are of a more or less uniform width. The abdominal sternites are pale-scaled except for a small dark median spot. The mesonotum is more or less uniformly covered with dark reddish-brown scales which become lighter posteriorly. The essential points regarding the male terminalia are outlined in the key.

The larvae are characterised by having the mid-frontal hairs of the head 2- to 3-branched and the inner frontal hairs 3- to 5-branched, the comb of the eighth segment composed of about 45–65 blunt-ended *scales*, the siphon tuft inserted at or slightly before the middle of the siphon, and the anal gills small and bulbous (shorter by far than the saddle). The siphon index is about 2·8 : 1.

Breeding places.—Brackish-water coastal marshes, subject to fluctuation in water levels.

Sardinian localities.—Cagliari, Capoterra and Pula as *Culex salinus* Fic. (Ficalbi, 1896); also as *Culex nemorosus* Meigen var. *salinus* Fic. (Ficalbi, 1899). Numerous localities around the coast. Found wherever brackish-water marshes exist; during periods of abundance, a most troublesome species to agricultural labourers.

Corsican localities.—Porto Vecchio, salt marshes and plain of the Stabiacco river (Galliard, 1927*a*); south of Biguglia (Edwards, 1928); Bevinco (2.vi.44), Travo * (19.v.44) and Prunette (22.v.44).

Aëdes geniculatus (Olivier) 1791. Encyclopédie Méthodique. Histoire Naturelle. Insectes. Panckoucke, Paris, **6**, p. 134 (*Culex*).

A highly distinctive species recognised by its conspicuous thoracic and leg markings. The latter are completely black (with a purplish lustre) except for the prominent white knee caps and basal two-thirds of the femora. The proboscis and palpi are black. The integument of the pleurae is black and covered with conspicuous patches of broad white scales. The mesonotum is clothed with yellowish-white scales, except for four broad stripes of tiny dark brown scales (sometimes the shorter lateral pair are fused with the median pair). The abdominal tergites are iridescent black except for lateral triangular patches of white scales. The wing scales are darkish. The male terminalia are characterised by long slender basistyles which have no basal and subapical lobes, and a long terminal spine on the dististyle which is about ⅓ the length of that appendage and apically somewhat bent. The stem of the claspette is much longer than the appendage. The paraprocts are apically heavily sclerotised and terminate in a single tooth. The lobes of the ninth tergite are crowned with 4–6 sabre-like setae.

The larvae are distinctive for the stellate hair tufts (three pairs dorsally and two ventrally) on the first seven abdominal segments. The anal gills are broad, somewhat oval, and the dorsal pair about 1½ times longer than the anal saddle. The comb of the eighth segment is composed of about 11–16 *spines* placed in a row. The pecten is short and does not reach to the siphon tuft which arises before the middle; siphon index about 2 : 1. The mid-frontal hairs of the head are 2-branched and the inner frontal hairs single. Likewise the antennal shaft hair is single and the antenna itself is devoid of spines.

Nothing resembling the closely related *Aëdes echinus* (Edwards, 1920*b*) has been seen. In the latter species, the scales of the scutellum are all broad, flat and white (rather than mostly or all narrow and ochreous as in *geniculatus*). Likewise the larvae differ in the form of the stellate hairs which are composed of very long, stout bristles, the median pairs being 8- to 10-branched (rather than short, slender and 4-branched as in *geniculatus*).

Breeding places.—Tree holes.

Sardinian localities.—Senorbí (23.viii.48), San Sperate * (22.iii.48) and Pattada * (24.ix.48).

Corsican localities.—Vizzavona (Galliard, 1927*a*); Ajaccio * (15.iii.44) and Mignattaja * (17.v., 4.vi., 14.vi.44).

Aëdes longitubus Cambournac 1938. The Proceedings of the Royal Entomological Society of London, Series B, **7**, p. 74.

There should be no trouble in distinguishing this mosquito from the other *Aëdes* under discussion either as an adult or as a larva. The former is notable for the completely white fifth tarsal segment on *all* legs and the latter for the conspicuously long black air tube. The difficulty comes in determining whether we are dealing with a distinct species or a form of *Aëdes pulchritarsis* (Rondani, 1872) which was described from the Tuscan coast on the nearby Italian mainland. I have tentatively assigned the Sardinian and Corsican specimens to *longitubus* because my larval material agrees with Cambournac's description and nothing is known about typical *pulchritarsis* larvae from Tuscany.

A number of forms pertaining to the *pulchritarsis* complex have been variously described as species or varieties, but Edwards (1932) considered most of them as local variants of the type form. These include: *Aëdes berlandi* Séguy (1921) from Paris and nearby Asnières, France (also reported from Pennaroya, Spain and Rabat, Morocco; Séguy, 1930*a*, 1930*b*); *Aëdes praeteritus* Séguy (1923*a*) from Le Pradet, Department of Var, in the south of France; *Finlaya versicolor* Barraud (1924) from Yusimarg, Kashmir; *Aëdes pulchritarsis* var. *asiaticus* Edw. (1926) from Drosh, Chitral, Pakistan; *Aëdes pulchritarsis* var. *stegomyina* Stackelberg & Montchadsky (Montchadsky, 1926) from Katta-Kourgan, Samarkand, and Old Bokhara, Uzbekistan (considered synonymous with *asiaticus* by Edwards, 1932); and *Aëdes simici* Baranoff (1927) from Schischevo near Skoplje, Yugoslavia (considered a synonym of the type form by Edwards, 1932). In addition, *Aëdes longitubus*, described from Aguas de Moura, Portugal, and also known from the Cavalaire region in the Department of Var, France (originally as *Aëdes heracleensis* Callot, 1944, 1945*a*) and Spain (Clavero, 1946) should be considered with this group.

The principal differences separating these forms are based on characters of scale coloration and arrangement on the mesonotum, abdominal tergites and legs. Unfortunately some of my material has the mesonotum badly brushed so that the ornamentation cannot be ascertained. Other specimens, however, are in better shape. Two males from Nuoro, Sardinia, appear to have the mesonotal design similar to *longitubus*, except that the median golden stripes extend posteriorly more than half way, are not separated by a line of white scales, and the sublateral pale spots are very indistinct. A female from Ajaccio, Corsica, has mesonotal markings completely different from those yet described. There is a broad median stripe of golden scales (not divided by a central line of white scales) extending posteriorly more than half way and disappearing imperceptibly into an area of dark brown scales before the antescutellar space. Lateral to the median stripe at the point of transition, there is an oval spot of dark brown scales (somewhat golden along the inner and anterior margin) surrounded by an area of whitish scales which extends posteriorly in a narrow line to the scutellum as well as latero-posteriorly to the wing base. A narrow line of whitish scales extends along the lateral margins of the mesonotum (somewhat in the form of arcs as in *longitubus*) and around the antescutellar space. The remaining background areas of the mesonotum are clothed with dark brown scales. A female from Prunette, Corsica, is similar except that the median golden stripe terminates posteriorly in a patch of whitish scales which have a tendency to form a line dividing the golden stripe medianly. The sublateral oval spots of dark scales are not as clearly defined, and the surrounding whitish scales do not extend posteriorly in a line to the scutellum. The bands of the abdominal tergites in all eight specimens before me reach the lateral margins, where they may or may not be expanded into triangular patches. In one male, they are expanded medianly as in *praeteritus*. The sternites are as in *longitubus*, black with a lateral white patch, although in some cases the latter almost touch in the middle, thus giving the appearance of basal bands, but with a dark central stripe running through as in *berlandi*. The femora are basally clothed with pale scales, which on the fore- and mid-leg predominate on the inner side and which on the hind leg almost completely encircle the femur except for a narrow dorsal stripe of dark scales. The femora and tibiae *may* or *may not* have a scattering of white scales on the black background. The tarsal markings are somewhat variable on the first two pairs of legs, but in general have the following pattern: fore-leg, segment 1 with basal and apical bands, segment 2 with basal and sometimes apical bands, segments 3 and 4 black, segment 5 white; mid-leg, segments 1 and 2 with basal and apical bands, segment 3 black or occasionally with basal band, segment 4 black, segment 5 white; hind leg, segments 1, 2 and 3 with basal and apical bands, segment 4 with basal band, segment 5 white. Two preparations of male terminalia from Sorgono, Sardinia, agree well with Cambournac's description except for the fact that the basal lobe carries only one prominent recurved seta rather than three, and thus they are similar to *berlandi*.

As indicated previously, the Sardinian larvae resemble those described under the name of *longitubus*. Some of the more important characteristics are as follows (based on seven larvae from Nuoro, Sardinia): head slightly wider than long; antenna about 3/4 length of head, with few minute spicules near base, shaft tuft 3-branched and inserted at about apical 2/3; frontal and post-clypeal head hairs well developed and much branched as follows: outer frontal 7–13, middle frontal 5–8, inner frontal 8–13 and post-clypeal 9–14; mid-frontals and post-clypeals are of equal length, inner frontals longer and outer frontals intermediate; lateral abdominal hairs long and double on segments 1 through 5 and single on 6; comb of eighth segment composed of 16–20 *spines* in a *triangular patch*, each spine with prominent central *sharply-pointed* tooth; siphon long, slender and black, index 6·5 to 7·6:1, tuft 3- to 5-branched, inserted at basal 1/4 or 1/3, more than double width of siphon at point of origin, pecten within basal 1/7 to 1/4 consisting of about 24–30 broad, somewhat *rectangular-shaped* plates having *fringe* of *tiny teeth along anterior* and *apical borders*; anal saddle almost same length as segment and enveloping more than half of it, upper caudal setae (2) 3- to 5-branched and 3/5 length of lower caudal setae (3), lower caudal setae single and 1/3 longer than siphon, ventral brush weak, about ten sparsely-branched tufts (two pre-cratal), anal gills elongate, sausage-shaped, the dorsal pair about 2/3 length of siphon and 4–6 times longer than saddle.

In addition to that of *longitubus*, the *pulchritarsis* complex has several other larval types which vary in the size of the gills, length of the siphon, form of the pecten elements, insertion of the siphon tuft, and number and form of the comb spines. All, however, are characterised by the conspicuous development of the post-clypeal and frontal head hairs. The essential points of interest concerning these larvae (where known) are summarised below.

1. *Aëdes pulchritarsis* var. *stegomyina*, Montchadsky (1926). Uzbekistan. The gills are unusually large, being double the length of the siphon, or 1/4 the length of the mature larval body. Siphon index 3 : 1. Pecten spines broadly pointed, with 3–6 basal denticles. Siphon tuft inserted just before middle. Comb of 6–10 (usually 8) spines in a row, with central tooth rather blunt. (I have seen a third-instar larva in the British Museum from Cyprus (7.iv.49, M. Aziz) which appears to be similar to Montchadsky's larva in some respects. The two combs vary from 8 to 10 spines and the central tooth of each spine is apically rounded. The gills are slightly longer than the siphon, which is also the case in third-instar *stegomyina* larvae. The siphon index is 3·5 : 1 and the tuft is inserted at the basal 3/8. The pecten " scales " are narrowly elongate, heavily sclerotised and with several secondary denticles; apex blunt, with transparent expansion bearing delicate fringe difficult to see.)

2. *Aëdes simici* Baranoff (1927). Serbia. Gills 3/4 length of siphon. Siphon index 4·5 to 5·1 : 1. Pecten spines figured as narrow, curved and pointed, with 2–3 basal denticles. Siphon tuft inserted just before the middle. Comb of 8 spines in a row, with central tooth sharp.

3. *Aëdes pulchritarsis*, Vogel (1929). Taurus region, Turkey. Gills unknown (lost). Siphon index 4·5 : 1. Pecten " scales " elongate and bluntly rounded, plate-like, with 1–5 (usually 3) basal teeth; two dark stripes extending from the base give the " scales " a two-pointed appearance. Siphon tuft inserted just before middle. Comb of 8 sharp-pointed spines in a row. Shakhov (1928) has described a similar larva from the Kharkov area, Ukraine. The pecten elements are figured as having a couple of basal denticles and the apex prolonged into two pointed teeth. This condition is apparently what Vogel saw, but whether the pecten elements are apically bifurcate or merely appear to be because of pigmentation is not certain; I am inclined to the latter view, as a somewhat similar condition exists in the Cyprus larva. The gills appear to be 3/4 length of siphon, the comb spines 8 in number in a row and the siphon tuft inserted at basal 1/3(?).

4. *Aëdes longitubus* Cambournac (1938). Portugal. Gills about 1/2 to 3/4 length of siphon (?), 4–6 times longer than anal saddle. Siphon index 5·5 to 8·1 : 1. Pecten " scales " subrectangular, somewhat rounded, with fringe of microscopic serrations along anterior and apical borders. Siphon tuft inserted at basal 1/3. Comb of 10–20 (average 16) sharp-pointed spines, forming a weak triangular patch. (The larva of *Aëdes heracleensis* (south of France) is similar.)

5. *Aëdes pulchritarsis*, Roman (1939, 1940). Lyons area, Rhone valley, France. Gills about 3/4 length of siphon (?), 1/7 length of body or double last segment. Siphon index not given, but the siphon is short. The pecten " scales," as figured, are somewhat subrectangular elements with three basal denticles. The scales are broad basally and heavily sclerotised; apically they are narrowed, blunt-tipped and membranous. No apical fringe comparable to that of the Cyprus larva is described; otherwise the scales seem to be of a similar type. Comb spines (8?) arranged in a row.

Because of the great variability present in the *pulchritarsis* complex, it is apparent that little can be done to resolve the confusion until larger series of adults associated with larvae have been collected. Particular attention should be paid to the type locality areas of *pulchritarsis* and *berlandi*. The morphology of the pecten elements of the siphon appears to be significant; these should be studied with great care as the details are difficult to make out even under high magnification.

Breeding places.—Tree holes.

Sardinian localities.—Cantoniera Lardine, Nuoro * (ii.47, larvae and reared males), Foresta di Ghivine, Dorgali (16.vii.48), Puddargiu region, Sorgono (6.vi.50), Budduso (24.ix.48) and Pattada (24.ix.48).

Corsican localities.—Porto Vecchio area, as *Aëdes pulchritarsis* (Galliard, 1928); Ajaccio (15.iii.44) and Prunette (22.v., 8.ix. 44).

Aëdes mariae (~~Edwards~~ & Et. Sergent) 1903. Annales de l'Institut Pasteur, **17**, p. 62 (*Culex*). /Edm.

The conspicuously speckled wings, femora and tibiae will distinguish *mariae* from all other Sardinian and Corsican species except *caspius*. From the latter it may be separated by the distinctly black and white abdominal bands, the black scaling of the legs and the ornamentation of the mesonotum. The mesonotum is largely clothed with golden scales, but with some white scales which may or may not form a sort of pattern, as follows: a patch across the anterior margin; just behind, a pair of small, sublateral oval spots; a second pair of median sublateral spots somewhat triangular in shape, which veer latero-posteriorly toward the wing bases and posteriorly (occasionally) toward the scutellum; a fringe around the antescutellar space; and a few scattered scales in the midline. Other specimens do not have a distinctive mesonotal pattern, the white scales being scattered rather haphazardly. The tarsi are conspicuous because of the apical and basal bands on some segments. The markings, while subject to slight variation, are as follows: fore-leg, segments 1 and 2 with basal and apical bands, segment 3 with basal band, and segments 4 and 5 black; mid-leg, segments 1, 2 and 3 with basal and apical bands, and segments 4 and 5 with basal bands; hind leg, segments 1, 2 and 3 with basal and apical bands, segment 4 with basal band, and segment 5 white. The white basal abdominal bands widen laterally and extend to the border of the tergites; in occasional specimens, there is also some indication of a widening at the midline and the more distal segments may have a few white scales on the apical margins. The proboscis usually has an accumulation of pale scales centrally which gives it the impression of being ringed, although black scales may intervene dorsally to break the ring. The male terminalia are similar to those of *longitubus*, but differ in the dimensions of the claspette stem and appendage, which are subequal in length or the appendage may be slightly shorter. The basal lobe is densely clothed with setae, some of which may be slightly stouter than the others, but these are not more heavily sclerotised and are not apically recurved as in *longitubus*. The subapical lobe in both species is hardly distinguishable and hence there might be some confusion with *geniculatus*; the stem of the claspette in the latter, however, is much longer than the appendage.

The larvae of *mariae* are most apt to be confused with those of *caspius* unless the breeding place is known. The siphon is somewhat cylindrical in shape, due to the fact that the apical and basal widths are closely approximate (index 1·2 : 1); moreover, the siphon is fairly short, index about 2 : 1 (average of 14 specimens, range 1·7–2·5). The siphonal tuft is longer and extends beyond the apex of the siphon. The tiny spicules seen on the anal saddle and the siphon (particularly at the apex) are much more conspicuous in *mariae*. In addition, the upper caudal tufts (2) of the anal segment are as long as, but more usually longer than, the siphon; they are shorter than the siphon in *caspius*.

The writer has been able to compare Sardinian specimens with larval material in the British Museum from other parts of the Mediterranean. While considerable local differences are present, the variation is so great that it is difficult to accept the fact that we are dealing with more than one species (two other names present in the literature are *Aëdes zammitii* (Theo.) (Theobald, 1903) from Malta and *Aëdes desbansi* Séguy (Séguy, 1923*a*) from Le Pradet, Var, France). Larvae from Beirut (P. J. Barraud) are notable for the great scarcity of spinelets on the antennae, as well as the great length of the pecten spines; the pecten spine ratio of the apical teeth (length of spine divided by basal width) is about 15 to 20 : 1. Specimens from Athlit, Palestine (P. A. Buxton), have similar pecten spines but the antennal spinelets are quite abundant; the siphons are also shorter, index 1·5 : 1 or less as compared with 1·6 to 1·9 : 1 (Beirut). Specimens from Malta are variable. Some have a pecten spine ratio of 7 : 1 and others 14 : 1; all have short siphons, about 1·3 : 1. Two specimens from Kavalla, Macedonia, are also intermediate in character, the antennae being less spiny than Sardinian specimens but not approaching the extreme condition in the Beirut material; the siphons are short, index 1·3 : 1 and 1·5 : 1. The pecten spine ratio is similar to that of Sardinian specimens. The latter have the regular spinose antenna typical of *Ochlerotatus* larvae, and the pecten spines are relatively short compared with the Beirut and Palestinian specimens, ratio about 6 to 7 : 1.

For further discussion of the subject, see Edwards (1928) and Senevet & Trensz (1932).

Breeding places.—Rock pools along coast containing concentrated sea water. Senevet & Trensz (1932) report salinities as high as 60 grammes NaCl per litre. The writer found a concentration of 5·17 per cent. chlorides in a larval habitat at Masua, Sardinia. The eggs are laid on the surface of the water, where they float singly without the aid of float chambers; their appearance is similar to other *Aëdes* eggs.

Sardinian localities.—Isola Razzoli (19.ix.48), Cala Lunga, Sant'Antioco (23.vi.50), Torre Pittinuri, Cuglieri * (10.ix.47), Pula * (1.viii.47), Isola Maddalena * (26.v., 18.ix.48), Corona Niedda * (22.vi.48), Isola Nibani * (21.v.48), Isola Le Camere * (21.v.48), Isola Soffi * (21.v.48), Tonara Saline, Stintino * (11.vi.48), Torre Columbaszie * (22.vi.48), Isola Mortorio * (21.v.48), Alghero * (18.vi.48), Marinella, Olbia * (20.v.48), Isola Pagliosa, Bosa * (18.vi.48), Isola Capuccini * (22.v.48), coast near mouth of Vignola river * (7.vi.48), Mercureddu, Calasetta, Sant'Antioco * (4.ix.49), Masua * (10.vi.51), Geremeas (31.vii.52), Santa Teresa Gallura * (27.viii.52).

Corsican localities.—I'lle Rousse (Edwards, 1928); Ajaccio (30.v.44).

Aëdes rusticus (Rossi) 1790. Fauna Etrusca, Sistens Insecta quae in Provinciis Florentina et Pisana. T. Masi, Liburni (Pisis), **2**, p. 333 (*Culex*).

A large brown mosquito, *rusticus* should ordinarily be recognised by the golden mesonotum with its four dark brown stripes (the lateral pair posterior) and the appearance of a median pale stripe on at least the posterior abdominal tergites (Marshall, 1938). These characters are not always reliable, but a diagnosis can be made from an examination of the posterior pronotum, which is clothed with broad flat scales, the upper ones being black and the lower ones whitish. A female from Alistro, Corsica, varies in having the background scales of the mesonotum yellowish-white rather than golden; the basal bands of the abdominal tergites are a similar colour and there is no indication of a median stripe, merely a few pale scales clustered at the apices of the distal tergites. Additional characteristics of this specimen are as follows. Broad pleural scales all greyish-white except for a patch of black scales on upper half of anterior and posterior pronotum. Palpi and proboscis black. Legs dark except for femora which have liberal scattering of pale scales, particularly on the undersides and basally, also few scales along tibiae; knees pale; anterior face, particularly of fore-femora, rather speckled. Wing with few pale scales at base of costa and veins four and six. The male terminalia of *rusticus*, among other things, are distinctive for the long golden-yellow hairs clothing the basistyles (Edwards, 1921).

The larvae are unique in having two pairs of siphon tufts, as well as 6–8 single setae arising from the dorsal surface of the siphon; these latter setae are slightly longer than the siphon width at their points of origin and the most distal of these are inserted at the apical 7/10 of the siphon. The pecten, occupying 54–70 per cent. of the siphon, consists of 19–24 spines, of which the distal one or two are markedly dissociated from the main row of spines and are simple (*i.e.*, devoid of basal denticles). The larger pair of siphonal tufts is inserted ventral to and about opposite the end of the main part of the pecten which occupies the basal 40 per cent. of the siphon; they are 5- to 8-branched and about 1·5 times longer than the siphon width at their points of origin. The smaller pair of tufts lies just dorsad of the pecten and opposite or slightly posterior to the larger tufts; they are 1- to 3-branched (usually 2) and about 1/2 to 2/3 the siphon width. The ventral valves of the siphon have a prominent hook-like terminal seta (9). The siphon index varies from 3 to 3·7 : 1. The comb of the eighth segment is composed of 12–16 *spines* in a somewhat triangular-shaped clump. The anal gills are shorter than the saddle and the latter does not quite encircle the segment (the saddle hairs are lost on my specimens). The ventral brush of the anal segment has 4 pre-cratal tufts (*i.e.*, tufts before the barred area). The frontal head hairs are stout, the middle and inner pairs being 1- to 3-branched.

I have seen nothing among the material from the islands resembling any of the following species: *Aëdes lepidonotus* Edw. (1920*b*), *refiki* Medschid (1928), *stampari* Apfelbeck (1929), *pseudorusticus* Callot (1945*a*) or *quasirusticus* Torres Cañamares (1951).

Breeding places.—Thought to be a single-generation species, the larvae are found in woodland pools and ditches containing leaves of deciduous vegetation (Marshall, 1938).

Sardinian localities.—Tandalo region, Budduso * (12.ii.48) and Ales * (17.ii.48).

Corsican localities.—Alesan swamp, Alistro (17.v.44).

Aëdes vexans (Meigen) 1830. Systematische Beschreibung der Bekannten Europäischen Zweiflügeligen Insekten. Schulz, Hamm, **6**, p. 241 (*Culex*).

Unless care is taken, adults of this species might be confused with some of the dark-legged *Aëdes*, as the tarsal rings are not very conspicuous. On the other hand, of the species with basal tarsal rings, only *cantans* might give some trouble; however, the indentations of the abdominal bands and the wing veins almost completely clothed with dark scales will distinguish *vexans* (a tiny patch of pale scales is present at the base of the costa). The male terminalia are noteworthy for the shape of the dististyle and the subterminal position of its spine.

I have no larvae in the material before me, but they are readily recognised by the characters indicated in the key.

Breeding places.—Flooded pastures, irrigation ditches and shallow temporary ground pools.

Sardinian localities.—Originally recorded from Sardinia as *Culex malariae* Grassi by Ficalbi (1899), but *Culex vexans* Mg. was also believed to be present. San Vero Milis (12.viii.48), Cabras (5.xi.48) and Orbai, Siliqua (2.xi.48).

Corsican localities.—Debbie marsh, Cateraggio (Galliard, 1927*a*); Calvi (Edwards, 1928); Prunette (30.vi., 23.viii.44), Ghisonaccia (7.viii., 4.ix.44) and Calvi (24.viii.52).

Aëdes vittatus (Bigot) 1861. Annales de la Société Entomologique de France, 4th series, **1**, p. 227 (*Culex*).

Like *aegypti*, this species is conspicuous for its white markings. As this is the first time the species has been reported from Corsica since its original discovery, a detailed description will be given. The proboscis is black rather than extensively pale in the middle as in African and some Indian specimens (Barraud, 1934; Edwards, 1941). The female palpi have a few white scales in the middle and many at the tip; in the male, there are four white rings, two on the long segment and one on the base of each of the two terminal segments. The antennae are white-scaled on the median and lateral margins of the torus, as well as on the first flagellar segment. The mesonotum is covered with narrow, curved, blackish-brown scales, on which are superimposed three pairs of white spots, the anterior pair being the largest. On the anterior margin of the mesonotum are two more ill-defined spots, and around the antescutellar space there are a few white scales. The scutellum is conspicuous for three clumps of broad white scales, the central clump also having a few blackish scales. The abdominal tergites have narrow basal bands of broad white scales which are discontinuous with the lateral spots. The wings are dark-scaled except for a tiny patch of white at the base of the costa. The legs have the femora speckled with white scales, a pre-apical ring and a few terminal white scales. The hind tibiae have a central ring which becomes more basal on the anterior legs. The tarsi have broad basal bands on the first three segments, the fourth segment of the hind leg is apically black and the fifth segment is white; the last two segments of the fore- and mid-legs are black. The male terminalia correspond with published descriptions of African and Indian material. The basistyle has a small apical tuft of hairs; the basal lobe is broad and covered with tiny hairs and spicules. The dististyle is apically expanded into a very large club-like process covered with fine hairs and tiny spicules, and carries a prominent subterminal hooked spine.

The larvae agree quite closely with descriptions published by Barraud (1934) and Hopkins (1936), the only notable difference from African material being the absence of spicules on the antennae. The middle and inner frontal hairs are single. The comb of the eighth abdominal segment is composed of about 8–10 *spines* in an irregular row. The siphon index is about 2·5 : 1. The pecten occupies about 70 per cent. of the siphon and has the apical spine (sometimes two) isolated; the latter has the basal denticles on both sides of the central tooth (as do some of the other pecten spines to a lesser extent) and hence resembles a comb spine. The siphon tuft is 3- to 4-branched, about equal in length to the width of the siphon at the tuft's point of origin, and is situated about opposite the end of the main part of the pecten, at about 2/3. The anal saddle is incomplete and the long tapered gills are at least triple the length of the saddle and longer than the siphon; the upper pair is slightly longer than the lower pair.

Breeding places.—The larvae are found in accumulations of water in rock holes along water courses. The pupae and larvae spend considerable time at the bottom of the pools.

Sardinian localities.—Flumendosa river, Villanova Tulo * (18.v.46); Picocca river, Cantoniera Monte Acuto (16, 22.vii.47); Picocca river, Cantoniera Ovile Cannas * (21.viii.47).

Corsican localities.—Originally described from Corsica by Bigot (1861) from a female collected by M. Bellier de la Chavignerie but no locality indicated. Gorge of the Bucalojo river, San Nicolao * (10.viii.44) and Gravone river, Cuttoli bridge, Ajaccio * (23.viii.52).

Genus CULEX.

Key to species of *Culex*.

Larvae.

1. Siphon hair tufts shorter than or about equal to width of siphon at their points of origin 2
   Siphon hair tufts distinctly longer than width of siphon at their points of origin 5
2. Siphon hair tufts paired, very short, 2- to 4-branched and arising beyond pecten; siphon slender, index 6 to 7 : 1 .... *brumpti* Galliard
   Siphon hair tufts longer, 6- to 10-branched; siphon more robust, index generally between 3 and 5 : 1 3

3. Siphon hair tufts more or less paired and arising beyond pecten; pecten spines rather widely spaced apically .... *theileri* Theo.

   Siphon hair tufts in ventral zigzag row, with first 2–3 tufts arising within pecten; pecten spines rather uniformly closely spaced 4

4.[4] Anal segment with upper caudal setae (2) 4-branched; gills about as long as saddle .... *laticinctus* Edw.

   Anal segment with upper caudal setae 2-branched; gills about 1/2 length of saddle .... *modestus* Fic.

5. Antennae with subterminal bristles (2) arising at 1/3 to 1/2 distance between terminal bristles and antennal shaft tuft. Anal gills long, tapering and about double length of saddle. Siphon with apico-dorsal setae (2) strong, well developed and curved (not hooked) .... *mimeticus* Noè

   Antennae with subterminal bristles arising adjacent to terminal bristles. Anal gills shorter than or about equal to saddle length (some *pipiens* have very long gills but they are rounded apically) 6

6. Head with mid-frontal hair tufts 3- to 5-branched (generally 4) and inner frontal tufts 4- to 6-branched (generally 5). Siphon usually short and more or less robust, sigmoid-shaped, index usually about 5·5:1 or less. Thoracic integument devoid of tiny spicules .... *pipiens* L.

   Head with mid- and inner frontal hair tufts usually 2-branched or single. Siphon long and slender, index usually 6 : 1 or above. Thoracic integument covered with tiny spicules 7

7. Siphon with apico-dorsal setae (2) large and hooked; siphon hair tufts at least twice width of siphon at their points of origin. Anal gills lanceolate and slightly longer than saddle; ventral pair longest .... *hortensis* Fic.

   Siphon with apico-dorsal setae short, weakly developed and straight; siphon tufts less than twice width of siphon at their points of origin. Anal gills bluntly pointed and about half as long as saddle; subequal ... *impudicus* Fic.

Adults.

1. Tarsi of hind legs with first segment distinctly shorter than tibia. Abdominal tergites with continuous lateral pale stripes .... *modestus* Fic.

   Tarsi of hind legs with first segment only slightly, if at all, shorter than tibia 2

2. Tarsi with pale rings. Wings with prominent patches of pale and dark scales .... *mimeticus* Noè

   Tarsi and wings dark (Note: *theileri* has some pale scaling along anterior margin of wing, but not forming spots) 3

3. Abdominal tergites with pale apical bands (sometimes reduced to lateral spots or completely absent) 4

   Abdominal tergites with pale basal bands 5

4. Tibiae of hind legs with prominent patch of white scales at apex. Palpi of males almost devoid of setae .... *hortensis* Fic.

   Tibiae of hind legs dark at apex or with only few pale scales. Palpi of males with terminal segments bearing many setae .... *impudicus* Fic.

5. Femora and tibiae of front and middle legs with distinct longitudinal white stripe .... *theileri* Theo.

   Femora and tibiae of front and middle legs without stripes 6

---

[4] Couplet doubtful (Senevet, 1947).

6. Proboscis with pale ring .... *brumpti* Galliard
   Proboscis dark 7
7. Abdominal tergites with broad white bands. Tibiae of hind legs with prominent apical pale spot .... *laticinctus* Edw.
   Abdominal tergites with very narrow yellowish-white bands. Tibiae of hind legs with less prominent apical pale spot .... *pipiens* L.

Males.[5]

1. Basistyles with scales; lobe of basistyles slightly beyond middle, and without a broad, flattened plate-like appendage .... *modestus* Fic.
   Basistyles without scales; lobe of basistyle situated well beyond middle ... 2
2. Basistyles with thumb-like sclerotic projection arising from outer margin adjacent to origin of dististyles .... *hortensis* Fic.
   Basistyles without this projection 3
3. Basistyles bulbous basally and adorned with many long conspicuous bristles. Dististyles contracting subapically and then expanding into " T " or pick-shaped process on which arises a hooked spine .... *impudicus* Fic.
   Basistyles elongate or triangular-shaped, adorned with less conspicuous setae. Dististyles not expanded apically 4
4. Dististyles expanded beyond middle. Phallosome with lower (inner) division a slender appendage expanded apically into a fan-shaped process .... *brumpti* Galliard
   Dististyles not expanded beyond middle. Phallosome with lower division otherwise 5
5. Dististyles bent sharply at right angles. Phallosome with lower (inner) division a slender, backwardly-directed, pointed process; upper (outer) division consisting of a large outwardly-directed tooth and about 4 smaller teeth .... *laticinctus* Edw.
   Dististyles curved gradually to apex. Phallosome otherwise 6
6. Phallosome with upper (outer) division broad, tube-like and apically truncate; lower (inner) division slenderly pointed posteriorly and then bent sharply at right angles apically .... *pipiens* L.
   Phallosome otherwise 7
7. Phallosome greatly divided, the two principal divisions (upper and lower) being subdivided themselves into several prominent curved teeth (about 6 altogether) .... *mimeticus* Noè
   Phallosome less complex, the upper (outer) division bearing 2–3 short teeth, and the lower (inner) being a simple, slender, backwardly-projecting pointed process .... *theileri* Theo.

Culex brumpti Galliard 1931. Annales de Parasitologie Humaine et Comparée, **9**, p. 134.

I have not seen the adult of this species, only the larvae, which I originally considered to be *Culex univittatus* Theo. According to Galliard (1931), *brumpti* is a fairly large mosquito. It may be recognised by the banded proboscis, uniformly dark-scaled wings, dark unbanded legs which have white spots at the femoro-tibial and tibio-tarsal joints, and lateral triangular white spots on the abdominal tergites. The male terminalia are characterised by the dististyles being short and stocky, expanded beyond the middle and then contracting apically. The phallosome is divided into two processes, the outer (upper) being robust basally and directed outwardly at an angle in the form of a sharp tooth, and the inner (lower) process consisting of a long, slender, curved arm expanded apically into a fan on which there are five longitudinal crests which terminate in spines.

---

[5] Adapted from Senevet (1949).

The larva may be distinguished from other *Culex* occurring in the islands by its relatively large size, slender air tube (siphon index about 6 to 7 : 1) and four to five pairs of very short siphonal hair tufts (2- to 3-branched and distinctly shorter than the width of the siphon at their points of origin). The body is not spiculose, except for a bit on the eighth segment. The middle and inner frontal head hairs are 2- to 3-branched. The antennal shaft hair is situated at 2/3 and the subterminal setae (2) are at the apex. The comb of the eighth segment is composed of 22–44 *scales*. The apico-dorsal setae (2) of the siphon are short, robust and straight. The pecten of the siphon occupies the basal 1/4 to 1/3, the spines varying in number from 8 to 11; the more distal spines are farther apart, are markedly curved and have many basal denticles which are difficult to count (Galliard says 10–12 denticles on distal spines and 3–5 on basal spines). The saddle encircles the anal segment. The gills are not quite as long as the dorsal border of the saddle. The upper caudal setae (2) of the anal segment consist of a pair of 4-branched hair tufts (one long, two shorter and one very short); the lower caudal setae (3) are single and as long as the siphon.

Breeding places.—Pools in river beds (Galliard, 1931).

Sardinian localities.—Solarusa * (4.viii.47).

Corsican localities.—Campo di Loro, Ajaccio,* Gravone river, Ajaccio * and Tavignano river, Aleria * (Galliard, 1927*a*, as *Culex perexiguus* Theobald; 1928, as *C. univittatus* Theobald; 1931, as *C. brumpti*).

Culex hortensis Ficalbi 1889. Bullettino della Società Entomologica Italiana, **21,** p. 27.

Like *Culex impudicus* Fic., this small mosquito has pale apical abdominal bands (sometimes indistinct), but may be recognised by the almost complete absence of setae on the male palpi and the presence of a distinct patch of white scales at the apex of the hind tibiae. The male terminalia are remarkable for the prominent, heavily sclerotised process near the apex of the basistyle, which is easily seen under the microscope in unmounted specimens.

The larvae belong to the group which has long, slender air tubes, the siphonal index varying from about 5 to 7 : 1 but generally above 6. The siphon carries about 10–12 long hair tufts (the basal ones being 3–4 times the siphon width at their points of origin) staggered irregularly along the ventral line; these tufts are 3- to 4-branched and as many as three may arise within the pecten. Near the apex of the siphon are 2–3 small, simple subdorsal hairs. The extremity of the siphon is characterised by a prominent pair of apico-dorsal setae (2) which are hooked; in addition, the distal ventral valve hair (9) is strong and hooked. The comb of the eighth segment is composed of about 30–40 *scales*. The saddle completely rings the anal segment. The anal gills are slender, lanceolate and slightly longer than the saddle; the ventral pair are the longest. The middle and inner frontal hair tufts of the head vary from 1 to 3 branches but are usually 2-branched. The integument of the thorax is covered with a dense mat of fine spicules. For a further discussion of the larva of *hortensis*, see Galliard (1927*b*).

Breeding places.—Mountain and lowland streams, pools of clear water containing vegetation as well as being shaded.

Sardinian localities.—The species was originally reported from the island by Ficalbi in 1899. Donigala di Tortoli (29.xii.48), Badde Suelzu, Monti (vi.,vii.50), San Priamo (17.x.47), Villagrande Strisaili (13.viii.47), Sarroch (28.v.46), Sassinosa region, Alto Flumendosa (29.viii.47, 4.i.48), Cantoniera Monte Acuto * (23.vii.47), Seui * (18.v.46), Nuragus * (19.vi.46), Villanovatulo * (18.v.46), Tertenia * (9.iii.48), Mandas * (23.iv.47), Nurachi * (19.vi.46), Sarcidano RR Station * (21.vi.46), Cantoniera Funtanamela * (21.vi.46), Sadali * (18.v.46), Isola di Asinara * (21.iii.48) and Monte Gonari, Orani * (7.ix.52).

Corsican localities.—Central mountain region—Corte, Tavignano valley, Forest of Campotile, Lake Nino (1,743 metres), Restonica valley and forest, Bergerie de Grotelle, Lake Melo, Vizzavona (Galliard, 1927*a*); Alesan swamp, Alistro * (17.v.44), Travo * (19.v.44), Prunelli * (19.v.44), Figaretto * (23.vi.44), Trinité * (24.vi.44), Prunette * (28.vii.44), Vizzavona * (14.viii.44), Casta * (6.ix.44); Argentella Mina, Calvi * (24.iii.52, Casalta), Corbara, I'lle Rousse * (26.iii.52, Casalta). Most of the 1944 and 1952 records are coastal.

Culex impudicus Ficalbi 1890. Bullettino della Società Entomologica Italiana, **22**, p. 81.

Originally described from Sardinia, *impudicus* is a small black mosquito with pale apical bands on the abdominal tergites, which sometimes are reduced to lateral spots only or else are completely absent. The pale spot at the apex of the hind tibia, typical of *hortensis*, is completely absent or else weakly defined. The male palpi are well clothed with setae. The prominently exposed basistyles (whence the specific name) adorned with many long bristles make gross identification of males of this species a simple matter.

The larvae are very similar to those of *Culex apicalis* Adams in having a long slender air tube which is expanded at the tip (siphon index varies from 7 to 9 : 1). Inasmuch as only *impudicus* adults have been identified in the Sardinian fauna (including reared material), the writer follows the suggestion of Galliard (1928) who queried the presence of *apicalis* in Corsica after being able to rear only *impudicus* adults from *apicalis*-like larvae. Larvae of *impudicus* are characterised by the presence of tiny spicules clothing the thorax. The comb of the eighth segment is composed of *scales*. The siphon carries 8–10 ventral hair tufts (not necessarily paired), usually commencing at the point where the pecten stops (rarely, the first pair may arise within the pecten); the tufts are usually 2- to 3-branched, but occasionally they are single; the tufts are much longer than the width of the siphon at their points of origin, and the basal ones may be slightly double the width. There are no pre-apical subdorsal setae on the siphon as in *hortensis*. The apico-dorsal setae (2) of the siphon are short, weakly developed and not hooked; the same is true of the distal ventral valve hair (9). The saddle completely rings the anal segment. The anal gills are short, subequal in length, bluntly pointed, and are only about half as long as the dorsal length of the saddle. The mid-frontal hair tufts of the head are single and the inner frontal tufts are usually 2-branched (range 1–3 branches).

The larva might occasionally be confused with that of *Culex sinaiticus* Kirkpatrick, but may be recognised by the spicules on the thoracic integument; *scales* instead of spines forming the eighth segment comb; and small, weakly developed apico-dorsal setae (2) of the siphon which are strong, well developed and slightly curved in *sinaiticus*.

Breeding places.—Mountain and lowland streams, pools, small ponds, rock pools. Fresh and stagnant water, generally with considerable vegetation and well shaded.

Sardinian localities.—Widespread in lowlands and mountains. Sassari (v., vi. 1890, Ficalbi); Villanovatulo (17.xi.48), Villagrande Strisaili (13.viii.47);

Cantoniera Monte Acuto * (23.vii.47), Arbus * (1.viii.47), Curcuris * (20.vi.46), Alà dei Sardi * (22.v.46) and Geremeas * (26.ix.52).

Corsican localities.—Numerous localities along east coast from Porto Vecchio to Bastia, also St. Florent in north and Ajaccio on west coast (Galliard, 1927*a*, as *Culex apicalis* Adams; 1928 as *C. impudicus*). Found in same areas in 1944 (THGA), also mountains back of Porto Vecchio, Palavesa region (26.viii.52).

Culex laticinctus Edwards 1913. Journal and Proceedings of the Asiatic Society of Bengal, (N.S.) **9,** p. 49.

This species has not been identified in Sardinia, and in the absence of specimens the writer has had to refer to the literature. According to Edwards (1921), *laticinctus* most closely resembles *Culex pipiens* L., but may be distinguished by the pure white bands on the abdominal tergites which are as broad or broader than the dark intervening bands. In addition, the male palpi are no longer than the proboscis and are less hairy than in *pipiens*. The male terminalia are said to have a dense patch of short hairs around the apex of the basistyle and near the lobe of the basistyle.

According to Senevet (1947), the larvae closely resemble those of *Culex modestus* Ficalbi in having a short siphon (index 2·8 to 4·6 : 1) with a ventral zigzag row of about 12 short hair tufts (6- to 8-branched and slightly shorter than the siphon at their points of origin); the most basal tuft generally arises opposite the fourth-from-last pecten tooth. The saddle is said to ring the anal segment completely. Senevet distinguishes the species, however, by the upper caudal setae (2) of the anal segment being 4-branched, whereas they are 2-branched in *modestus*. Other characters which might be of value include the size of the gills which are about as long as the saddle, the size of the saddle which is figured by Séguy (1924) and Hopkins (1936) as being longer than broad, and the shape of the saddle which Hopkins says only partially surrounds the anal segment.

Breeding places.—Unknown in the islands, but in Egypt it is found in artificial pools, tanks and barrels in gardens (Hopkins, 1936).

Sardinian localities.—None.

Corsican localities.—Lucciana (Galliard, 1927*a*).

Culex mimeticus Noè 1899. *In* Ficalbi, Bullettino della Società Entomologica Italiana, **31,** p. 224.

Recognition of *mimeticus* adults is simple, as they are the only known local *Culex* having banded legs, spotted wings caused by light and dark scales grouped in patches along the veins, and a banded proboscis. The male terminalia have the most complex phallosome of those *Culex* under discussion; the inner (lower) division extends backwards and curves sharply at right angles apically in the form of a tuberculated tooth or teeth, and the outer (upper) division consists of three long teeth curved outwardly and a fourth recurved towards the base.

The larvae are relatively large and, like *Culex theileri* Theo., have *spines* instead of scales composing the eighth segment comb. The integument of the thorax is not spiculose. The siphon is long, but not as slender as that of *hortensis* or *impudicus*, index about 6 : 1 (range 5·5 to 6·2 : 1). The ventral siphonal hair tufts are about 10 in number, arising beyond the pecten which has 14–17 closely grouped spines having about 10 basal denticles; the basal tufts are 4- to 5-branched and long, about twice the width of the siphon at their points of origin. The apico-dorsal setae (2) of the siphon are strong, prominent and curved (length about 3/4 apical width of siphon). The saddle completely rings the anal segment. The gills are long and tapering, about twice the length of the saddle. The mid-frontal head hairs are 2-branched and the inner frontal tufts are 3- to 4-branched; the post-clypeals are 2- to 4-branched. The subterminal bristles (2) of the antennae arise from 1/3 to 1/2 the distance between the terminal bristles and the antennal tuft.

The closely related *Culex prosecutor* Séguy (1927) (= *C. pseudomimeticus* Séguy, 1925), known from the Rhone delta, Camargue, France, may be recognised as follows. The siphon is fairly long and slender, index 5 : 1; the pecten has 14 spines which have two very long basal teeth and an apical fan-like fringe of about 9 teeth. The siphon tufts (14) form a more or less straight ventral line, occupying most of the siphon with the first three tufts arising within the pecten; they are about 3- to 4-branched and the longest are 2–3 times the greatest width of the siphon. The eighth segment comb consists of two to three rows of blunt-ended *scales*, each having an apical fringe of hair-like teeth. The saddle completely rings the anal segment. The gills are long and tapering; the ventral pair are illustrated by Séguy as being the longer and are more than 1·5 times the dorsal saddle length.

Breeding places.—The larvae breed in streams and torrents which are drying up and contain growths of *Spirogyra*; they are frequently found with *Anopheles hispaniola* and the writer took them with *Anopheles superpictus* in Corsica.

Sardinian localities.—San Gregorio (1.xii.48), Cantoniera Monte Acuto (11.vii.47), Senorbí (25.viii.48), San Priamo (21.x.47), San Andrea Frius * (25.viii.50), Tertenia * (6.ix.50), Nebida * (30.vii.47), Paulilatino * (30.vii.47), Geremeas * (adults and larvae, June–Sept.52).

Corsican localities.—Porto Vecchio, Ajaccio * (Galliard, 1928); Bravone river, Bravona * (4.ix.44); Gravone river, Cuttoli bridge, Ajaccio * (23.viii.52).

Culex modestus Ficalbi 1889. Bullettino della Società Entomologica Italiana, **21**, p. 93.

This species has not been recognised in any material from Sardinia, and the writer has had to rely on published descriptions. Adults of *modestus* are small and may be identified by the first tarsal segment of the hind leg being much shorter than the tibia. Like *hortensis*, the palpi of the male are almost devoid of setae. The male terminalia are characterised by the presence of scales on the outer side of the basistyle and the lobe of the basistyle being situated only slightly more than halfway towards the apex and devoid of a flattened plate (Edwards, 1921).

The larvae have a relatively short stubby siphon (index 3·5 to 5 : 1), carrying 10 short hair tufts in a ventral zigzag row (tufts 6- to 8-branched and no longer than the width of the siphon at their points of origin); the first of these tufts are vaguely paired and arise within the pecten. The saddle is as long as it is wide and completely rings the anal segment. The upper caudal setae (2) of the anal segment are 2-branched and the lower caudal setae (3) are single. The gills are short and about one-half the length of the saddle (Senevet, 1947).

Breeding places.—Said to be marshes (Ficalbi, 1889). Senevet (1947) mentions ponds, flooded low areas and rivers; both brackish and fresh waters.

Sardinian localities.—None.

Corsican localities.—Porto Vecchio (Galliard, 1928); Porto (Edwards, 1928).

Culex pipiens L. 1758. Systema Naturae per Regna Tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edition. L. Salvii, Holmioe, **1**, p. 602.

The adults are drab-looking dark brown insects with no particular marks of distinction, except for the fact that the yellowish-white basal bands of the abdominal tergites are very narrow (1/4 or less the length of the tergite). All of the specimens examined appear to refer to *pipiens* rather than to *Culex molestus* Forsk., as the pale knee spots are prominent; the dark blackish-brown scales of the abdominal tergites and legs have a metallic blue iridescence; the abdominal sternites have dark scales laterally and in a median spot; and the combined length of the first four segments of the male palpus exceeds that of the proboscis. The male terminalia are characterised by the inner (lower) division of the phallosome being slender and somewhat sickle-shaped (it is directed straight backwards and then outwardly bent, usually at right angles); the outer (dorsal) division of the phallosome is shaped like a truncate tube and is directed outwardly at an angle. In 240 slide preparations examined, the inner division of the phallosome in no case extended laterally beyond the outer division as appears to be the case in American specimens (Rozeboom, in Mattingly & others, 1951). Setal counts of 260 male ninth tergite lobes gave a mean figure of 8·76 setae per lobe, with the extremes varying from 4 to 18; individual specimens varied considerably in the counts on the two lobes, *e.g.*, 6–10, 8–13.

The larvae may be recognised by the greater branching of the head hairs, the mid-frontal tufts being 3- to 5-branched (generally 4) and the inner frontal tufts 4- to 6-branched (generally 5). The thoracic integument is devoid of spicules. The comb of the eighth abdominal segment is composed of about 40–50 *scales*. The siphon is sigmoid-shaped, and beyond the pecten carries 3–5 pairs (usually 4) of subventral tufts, the penultimate being out of line; these tufts are 2- to 3-branched and are longer than the width of the siphon at their points of insertion (except the penultimate tufts which equal the width of the siphon). The apico-dorsal setae (2) of the siphon are relatively short and only slightly curved. The siphon index in specimens seen varies between 4 and 7 : 1, but is usually about 5·5 : 1. The saddle completely rings the anal segment, and the anal gills are longer than the dorsal side of the saddle. For further information regarding *pipiens* and *molestus*, reference should be made to Marshall (1938) and Mattingly & others (1951).

Breeding places.—Practically any type of aquatic situation except the extremely salty; found in both fresh and foul water, Senevet (1947) mentions a salt tolerance up to 14 grammes per litre.

Sardinian localities.—First reported by Ficalbi in 1889. It is widespread and common throughout the island, close to and distant from human habitations.

Corsican localities.—Widespread and common (Galliard, 1927*a*).

Culex theileri Theobald 1903. A Monograph of the Culicidae or Mosquitoes. The British Museum (Natural History), London, **3**, p. 187.

This is a fairly large mosquito, as the present species of *Culex* go. The general coloration is brown. The abdomen has prominent pale basal bands which are yellowish-white in colour. The pale scaling of the first two to three abdominal tergites is restricted to the midline; in subsequent tergites it forms broad bands which are rounded to triangular in shape and may occupy close to one-half the tergite at their widest point. The seventh and eighth tergites have pale scales apically as well, the latter being almost completely pale. The dark scales of the abdomen are brownish rather than black. The presence of longitudinal white stripes in the femora and tibiae, of the first and second pairs of legs particularly, is perhaps the most distinguishing feature of the species. The proboscis has an admixture of pale and dark scales, the former predominating below. The palpi have some white scales dorsally. The wings also carry some pale scales along the posterior border of the costa, the subcosta and the anterior border of the first vein; otherwise the wing scales are dark. The male terminalia are distinguished by the make-up of the phallosome.

The larvae are fairly large. The middle and inner frontal head hairs are 2- to 3-branched and the post-clypeals are single or 2-branched. The subterminal bristles (2) of the antennae arise adjacent to the terminal bristles. Spicules are not present on the thoracic integument, although a few are present on the eighth segment. The comb of the eighth segment is composed of about 30 *spines*. The siphon index is about 5·5 : 1. The pecten occupies the basal third of the siphon and is composed of about 10 fairly widely-spaced spines, the more distal being markedly curved and the remainder somewhat recurved or undulating in outline, bearing 2–4 small basal denticles. Siphon tufts are 9–10 in number, are located ventrally well beyond the pecten and in general are paired; they are about as long as the siphon width at their points of origin and are 8- to 10-branched (except for the apical pair which are 4-branched). The apico-dorsal setae (2) of the siphon are slightly curved and small (less than 1/4 apical width of siphon). The saddle completely rings the anal segment. The gills are subequal, lanceolate and slightly shorter than the dorsal length of the saddle.

Breeding places.—Streams, swamps, ponds and pools; usually in stagnant water.

Sardinian localities.—Isalle river valley near Orune (4.vii.47), Arborea * (2.viii.47), Serrenti * (12.viii.47), Paringianu * (30.vii.47), Donori * (5.viii.47), Muravera (17.x.47), Geremeas * (larvae and adults, July–Sept.52), Cabras * (15.ix.52).

Corsican localities.—Fairly common—Ajaccio, Sale Lagoon at Ghisonaccia, Lucciana plain near Grand Fossone (Galliard, 1927*a*).

Summary.

Field observations on the Culicidae of Sardinia and Corsica were undertaken in 1944, during the period 1946 to 1950, and again in 1952. A total of 52 species are recorded as being present, 46 of which are known from Corsica and 35 (exclusive of Dixinae) from Sardinia. The faunal list of the latter island has been increased by 20 new records and that of Corsica by three. The total number of species by genus is as follows: *Dixa* (7), *Chaoborus* (3), *Anopheles* (12), *Uranotaenia* (1), *Culiseta* (6), *Orthopodomyia* (1), *Taeniorhynchus* (2), *Aëdes* (12) and *Culex* (8).

The previously unknown male of *Taeniorhynchus buxtoni* Edwards is described from Sardinian material. *Culiseta litorea* (Shute), heretofore known only from England, was found in two localities in Sardinia. *Aëdes vittatus* (Bigot) was rediscovered in Corsica, 83 years after its original description.

Keys are given to subfamilies, genera and species. Critical notes on species differentiation are included and biological characteristics briefly discussed.

Acknowledgements.

I should like to take this opportunity to express my appreciation to the authorities of the British Museum of Natural History, the Johns Hopkins University School of Hygiene and Public Health, and the Museum of Comparative Zoology, Harvard University, for permission to use their departmental and library facilities. My thanks are also due to Mr. P. F. Mattingly, of the British Museum, for kindly reading and criticising the manuscript.

References.

APFELBECK, V. (1929). Neue Culiciden aus Bosnien und Dalmatien.—Konowia, **8,** pp. 286–292.

BARANOFF, N. (1927). Eine neue *Aëdes*-Art aus Süd-Serbien (Dipt., Culic.).—N. Beitr. syst. Insektenk., **4,** pp. 15–16.

BARRAUD, P. J. (1924). A new mosquito from Kashmir and the North-West Frontier Province.—Indian J. med. Res., **12,** pp. 73–74.

BARRAUD, P. J. (1934). The fauna of British India including Ceylon and Burma. Diptera. Vol. V. Family Culicidae. Tribes Megarhinini and Culicini. —xxviii + 463 pp., 8 pls., 106 figs., 1 fldg. map. London, Taylor & Francis.

BATES, M. (1939). Variation in the antepalmate hairs of larvae of the *Anopheles maculipennis* complex.—Riv. Malariol., **18,** pp. 299–312.

BATES, M. (1941). Field studies of the Anopheline mosquitoes of Albania.—Proc. ent. Soc. Wash., **43,** pp. 37–58.

BELKIN, J. N. (1950). A revised nomenclature for the chaetotaxy of the mosquito larva (Diptera: Culicidae).—Amer. Midl. Nat., **44,** pp. 678–698.

BELKIN, J. N. (1952). The homology of the chaetotaxy of immature mosquitoes and a revised nomenclature for the chaetotaxy of the pupa (Diptera, Culicidae).—Proc. ent. Soc. Wash., **54,** pp. 115–130.

BIGOT, M. J. (1861). Trois diptères nouveaux de la Corse.—Ann. Soc. ent. Fr., (4) **1,** pp. 227–229.

BRUMPT, E. (1925). Les anophèles de Corse.—Bull. Acad. Méd., Paris, (3) **94,** pp. 811–815.

BUXTON, P. A. (1924). Applied entomology of Palestine, being a report to the Palestine government.—Bull. ent. Res., **14,** pp. 289–340.

CALLOT, J. (1944). Sur un nouveau moustique arboricole: *Aëdes* (*Finlaya*) *heracleensis* sp. nov.—Bull. Soc. Path. exot., **37,** pp. 56–59.

CALLOT, J. (1945*a*). A propos de *Aëdes* (*Finlaya*) *heracleensis* Callot 1944.—Ann. Parasit. hum. comp., **20,** pp. 93–94.

CALLOT, J. (1945*b*). Diptères nématocères piqueurs d'Auvergne.—Rev. Sci. nat. Auvergne (N.S.), **11,** fasc. 1–2, pp. 28–36.

CAMBOURNAC, F. J. (1938). *Aëdes* (*Ochlerotatus*) *longitubus*, a new species from Portugal. (Diptera, Culicidae).—Proc. R. ent. Soc. Lond., (B) **7,** pp. 74–80.

CATANEI, A. (1925). Anophèles de hautes régions de la Corse. Presence d'*A. bifurcatus* L. et d'*A. plumbeus* H. et S. dans l'île.—Bull. Soc. Path. exot., **18,** pp. 655–657.

CHRISTOPHERS, S. R. (1933). The fauna of British India including Ceylon and Burma. Diptera. Vol. IV. Family Culicidae. Tribe Anophelini.—xi + 371 pp., 3 pls., 53 figs. London, Taylor & Francis.

CLAVERO, G. (1946). Aedinos de España.—Rev. Sanid. Hig. públ., Madr., **20,** repr. 28 pp., 39 pls.

DEL VECCHIO, G. (1939). Sulle varietà di *A. claviger* (*bifurcatus*). Nota I.—Riv. Parassit., **3,** pp. 27–37.

EDWARDS, F. W. (1920*a*). The British Chaoborinae and Dixinae (Diptera, Culicidae).—Ent. mon. Mag., **56,** pp. 264–270.

EDWARDS, F. W. (1920*b*). Mosquito notes.—Bull. ent. Res., **10,** pp. 129–137.

EDWARDS, F. W. (1921). A revision of the mosquitos of the palaearctic region.—Bull. ent. Res., **12,** pp. 236–351.

EDWARDS, F. W. (1926). Una revisione delle zanzare delle regioni paleartiche.—Riv. Malariol., **5,** pp. 253–285, 392–466, 613–652.

EDWARDS, F. W. (1928). The nematocerous Diptera of Corsica.—Encycl. ent. (B) II, Diptera, **4,** pp. 157–189. Paris, Lechevalier.

EDWARDS, F. W. (1930). The British species of *Chaoborus* and *Mochlonyx* (Diptera, Culicidae).—Ent. mon. Mag., **66,** pp. 163–165.

EDWARDS, F. W. (1932). Diptera. Fam. Cullicidae.—Genera Insect., **194,** 258 pp., 5 pls. Brussels: Wytsman.

EDWARDS, F. W. (1941). Mosquitoes of the Ethiopian region. III. Culicine adults and pupae.—viii + 499 pp., 4 pls., 184 figs. London, Brit. Mus. (Nat. Hist.).

FICALBI, E. (1889). Notizie preventive sulle zanzare italiane. VI^a nota preventiva. Quistioni zoologiche intorno al *Culex pipiens* e descrizione di una specie nuova (*Culex phytophagus*).—Bull. Soc. ent. ital., **21,** pp. 124–131.

FICALBI, E. (1890). Notizie preventive sulle zanzare italiane. VII^a nota preventiva. Descrizione di una specie nuova. Zanzara impudica, *Culex impudicus*, sp. n.—Bull. Soc. ent. ital., **22,** pp. 81–84.

FICALBI, E. (1896). Notizie sulle zanzare italiane. IX^a nota. Descrizione di una specie nuova. Zanzara delle saline, *Culex salinus*, sp. n.—Bull. Soc. ent. ital., **28,** pp. 29–32.

FICALBI, E. (1899). Venti specie di zanzare (Culicidae) italiane, classate e descritte e indicate secondo la loro distribuzione corologica.—Bull. Soc. ent. ital., **31,** pp. 46–234.

GALLIARD, H. (1927*a*). Note sur les culicinés de Corse.—Ann. Parasit. hum. comp., **5,** pp. 97–104.

GALLIARD, H. (1927*b*). Note sur les larves de *Culex hortensis* Ficalbi et *Culex apicalis* Adams.—Bull. Soc. Path. exot., **20,** pp. 609–613.

GALLIARD, H. (1928). Quelques culicidés nouveaux pour la Corse en particulier *Culex impudicus* Ficalbi.—Ann. Parasit. hum. comp., **6,** pp. 451–454.

GALLIARD, H. (1931). *Culex brumpti*, n. sp. moustique nouveau trouvé en Corse.—Ann. Parasit. hum. comp., **9,** pp. 134–139.

GALLIARD, H. & SAUTET, J. (1934*a*). Note préliminaire sur les races d'*Anopheles maculipennis* de Corse.—Bull. Soc. Path. exot., **27,** pp. 30–34.

GALLIARD, H. & SAUTET, J. (1934*b*). *Anopheles sacharovi* Favr (*elutus* Edw.) et *A. maculipennis* var. *labranchiae* dans leurs rapports avec le paludisme en Corse.—Bull. Soc. Path. exot., **27,** pp. 855–857.

GALLIARD, H. & SAUTET, J. (1935). Nouvelle contribution à l'étude de l'anophélisme en Corse. Les variations saisonnières de l'indice maxillaire.—Bull. Soc. Path. exot., **28,** pp. 453–456.

GIL COLLADO, J. (1930). Datos actuales sobre la distribución geográfica de los culícidos españoles.—Eos, **6,** pp. 329–347.

HACKETT, L. W. & MISSIROLI, A. (1935). The varieties of *Anopheles maculipennis* and their relation to the distribution of malaria in Europe.—Riv. Malariol., **14,** pp. 45–109.

HADJINICOLAOU, J. (1938). Observations of *Anopheles marteri* S. & P. (Diptera, Culicidae).—Riv. Malariol., **17,** pp. 44–50.

Hopkins, G. H. E. (1936). Mosquitoes of the Ethiopian region. I. Larval bionomics of mosquitoes and taxonomy of culicine larvae.—250 pp., 158 figs. London, Brit. Mus. (Nat. Hist.).

Jaujou, C., Camain, R. & Adam, J. P. (1950). Plan de mise en valeur de la Corse. Rapport sur l'activité du service antipaludique en 1949.—75 pp. Ajaccio, Impr. Siciliano.

Jaujou, C., Michel, L. & Hamon, J. (1951). Plan de mise en valeur de la Corse. Rapport sur l'activité du service antipaludique en 1950.—63 pp. Paris, Alépée et Cie.

La Face, L. (1929). Morfologia delle larve anofeliche e descrizione delle specie italiane.—Riv. Malariol., **8**, pp. 538–568.

Langeron, M. (1925). Présence en Corse de l'*Aëdes* (*Stegomyia*) *argenteus* (Poiret 1787).—Bull. Soc. Path. exot., **18**, pp. 723–725.

Langeron, M. & Galliard, H. (1933). Deux types de larves d'*Anopheles* nouveaux pour la Corse.—Ann. Parasit. hum. comp., **11**, pp. 93–95.

Laven, H. (1950). Der Schuppenindex als Unterscheidungsmerkmal der Arten in der *Anopheles maculipennis*-Gruppe.—Z. Tropenmed., **2**, pp. 111–124.

Laveran, A. (1900). Paludisme et moustiques; quelques faits recueillis dans le midi de France et en Corse.—C. R. Soc. Biol., Paris, **52**, pp. 987–989.

Logan, J. A. & others (1953). The Sardinian project: an experiment in the eradication of an indigenous malarious vector.—Amer. J. Hyg. Monogr. Ser., no. 20, xxix + 415 pp., frontis., 56 pls., 37 figs., 1 map. Baltimore, Md., Johns Hopkins Pr.

Marshall, J. F. (1938). The British mosquitoes.—xi + 341 pp., 20 pls., 172 figs. London, Brit. Mus. (Nat. Hist.).

Marshall, J. F. & Staley, J. (1933). *Theobaldia* (*Culicella*) *litorea* (Shute) n. sp. (Diptera, Culicidae).—Parasitology, **25**, pp. 119–126.

Mattingly, P. F. & others (1951). The *Culex pipiens* complex.—Trans. R. ent. Soc. Lond., **102**, pp. 331–382.

Medschid, — (1928). Über *Aëdes lepidonotus* Edw. und *Aëdes refiki* n. sp.—Arch. Schiffs-u. Tropenhyg., **32**, pp. 306–315.

Missiroli, A. (1927). La prevenzione della malaria nel campo pratico.—Riv. Malariol., **6**, pp. 501–572.

Missiroli, A. (1944). La malaria nel 1944 e misure profilattiche previste per il 1945.—R. C. Ist. sup. Sanit., **7**, pp. 616–641.

Montchadsky, H. S. [Monchadskiĭ, A. S.] (1926). Larva of *Aëdes* (*Ochlerotatus*) *pulchritarsis* Rond. var. *stegomyina*, Stack. & Montch. nov., from Turkestan.—Bull. ent. Res., **17**, pp. 151–157.

Peus, F. (1934*a*). Über einige bisher nicht oder wenig bekannte *Dixa*-Arten der palaearktischen Fauna (Diptera: Nematocera).—Arb. morph. taxon. Ent. Berl., **1**, pp. 195–204.

Peus, F. (1934*b*). Zur Kenntnis der Larven und Puppen der Chaoborinae (Corethrinae auct.). (Morphologie, Ökologie, Entwicklungsbiologie).—Arch. Hydrobiol., **27**, pp. 641–668.

Roman, E. (1939). Moustiques arboricoles de la région lyonnaise. La larve et la nymphe d'*Aedes pulchritarsis*.—J. Méd. Lyon, **20**, pp. 153–160.

Roman, E. (1940). Sur quelques moustiques rares de la région lyonnaise (Dipt. Culicidae).—Bull. Soc. ent. Fr., **45**, pp. 69–72.

Séguy, E. (1921). Description d'un nouveau moustique français du groupe de l'*Aedes mariae* et synopsis des espèces de ce groupe.—Bull. Soc. ent. Fr., **26**, pp. 192–195.

Séguy, E. (1923*a*). Remarques sur quelques moustiques.—Ann. Soc. ent. Fr., **92**, pp. 205–208.

Séguy, E. (1923*b*). Histoire naturelle des moustiques de France. Encycl. prat. Nat., **14**, ii + 225 pp., 201 figs. Paris, Lechevalier.

Séguy, E. (1924). Les moustiques de l'Afrique mineure, de l'Égypte et de la Syrie.—Encycl. Ent., (A) **1**, 257 pp., 29 pls., 106 figs., 10 maps. Paris, Lechevalier.

Séguy, E. (1925). Notes sur les moustiques de l'Afrique mineure, de l'Égypte et de la Syrie. I.—Encycl. Ent., (B) II, Diptera, **2**, pp. 13–21. Paris, Lechevalier.

Séguy, E. (1927). Notes sur les moustiques de l'Afrique mineure, de l'Égypte et de la Syrie. II.—*Op. cit.*, **4**, pp. 27–28.

Séguy, E. (1930*a*). Notes sur les moustiques. III.—*Op. cit.*, **5**, pp. 177–178.

Séguy, E. (1930*b*). Contribution à l'étude des diptères du Maroc.—Mém. Soc. Sci. nat. Maroc, **24**, 206 pp.

Senevet, G. (1935). Les Anophèles de la France et de ses colonies. 1re partie. France, Corse, Afrique, Madagascar, La Réunion.—Encycl. Ent., (A) **19**, 361 pp., 144 figs. Paris, Lechevalier.

Senevet, G. (1947). La genre *Culex* en Afrique du nord. I. Les larves.—Arch. Inst. Pasteur Algér., **25**, pp. 107–136.

Senevet, G. (1949). Le genre *Culex* en Afrique du nord. II. Les armures génitales mâles.—Arch. Inst. Pasteur Algér., **27**, pp. 48–65.

Senevet, G. & Trensz, A. (1932). A propos de l'*Aëdes mariae* (Sergent, 1903).—Bull. Soc. Path. exot., **25**, pp. 702–709.

Shakhov, S. (1928). *Anopheles plumbeus* Hal. in Ukraine.—Rev. Microbiol., Saratov, **7**, pp. 23–34. [In Russian with English summary, p. 137.]

Shute, P. G. (1928). A new variety of *Culicella morsitans* (Theobald) (Diptera).—Entomologist, **61**, p. 186.

Spanedda, A. (1940). Tipi di anophelini esistenti in provincia di Cagliari.—Rass. med. Sarda, **42**, no. 4 pp. 1–5.

Theobald, F. V. (1903). A monograph of the Culicidae or mosquitoes, **3**, p. 252. London, Brit. Mus. (Nat. Hist.).

Theodor, O. (1925). Observations on Palestinian *Anopheles*.—Bull. ent. Res., **15**, pp. 377–382.

Torres Cañamares, F. (1945). Contribución al conocimento del *Anopheles claviger* Mg. de España. (Dip. Cul.).—Eos, **20**, pp. 233–245.

Torres Cañamares, F. (1951). Una nueva especie de *Aedes* (Dipt. Cul.).—Eos, **27**, pp. 79–92.

Toumanoff, C. & Rageau, J. (1949). Rapport sur l'enquête malariologique effectuée en Corse (15 octobre–15 novembre 1947).—Rec. Inst. nat. Hyg., **3**, vol. 3 pp. 1029–1094.

Ungureanu, E. & Shute, P. G. (1947). The value of the wing scales as an aid to the taxonomy of adult *Anopheles maculipennis*.—Proc. R. ent. Soc. Lond., (B) **16**, pp. 79–85.

van Thiel, P. H. (1941). The identification of the pupae of *Anopheles superpictus*, *Anopheles bifurcatus* and of the different biotypes of *Anopheles maculipennis*.—Acta leidensia, **15–16**, pp. 283–288.

Vogel, R. (1929). *Aëdes pulchritarsis* Rondani (Culicidae) ein Baumhöhlenbrüter.—Int. Rev. Hydrobiol., **21**, pp. 161–170.

FURTHER TRIALS WITH PARATHION DUSTS AGAINST *EURYGASTER INTEGRICEPS* PUT. (HEMIPTERA, PENTATOMIDAE).

By A. S. Talhouk.*

Section of Entomological Research, Ministry of Agriculture,
Damascus, Syria.

In 1950, a series of laboratory and field trials were carried out in Syria with parathion dusts against *Eurygaster integriceps* Put. (Talhouk, 1951). The results of these trials were considered sufficiently encouraging for the Ministry of Agriculture to carry out further work with a view to determining the best time, and rate, of application of the dust, and the most satisfactory type of duster.

Trials in 1951.

The effect of different rates of application.

Field trials were performed on wheat in the district of Djebel el-Akrad on the Syrian-Turkish frontier, where the insects occur in variable numbers every year. Three plots (A, B & C) were dusted on 11th May and a fourth plot (D) was left untreated. Plots A and B each measured 25 × 100 metres, plot C 25 × 80 metres, whilst plot D, the control, measured 25 × 330 metres and extended alongside and parallel to plots A, B and C (fig. 1).

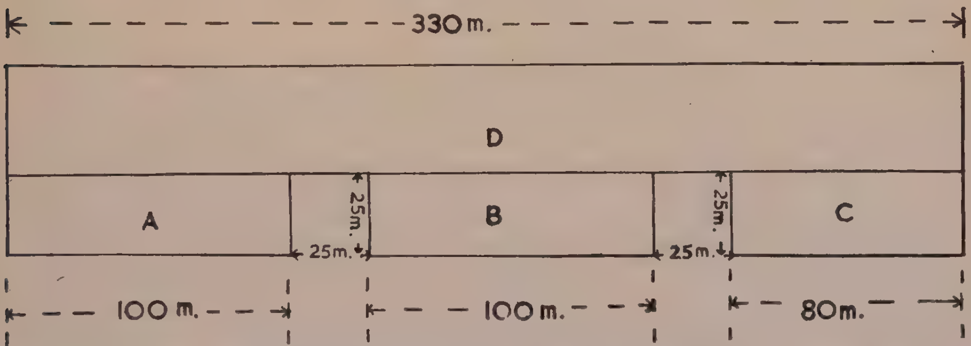


Fig. 1.—Lay-out of 1951 trials with parathion dusts. Treated plots: A, B, C. Control plot: D.

A dust containing 0·75 per cent. parathion was applied to the three plots at 40, 20, and 10 kg. per hectare respectively.

The dust was applied by means of a 6 h.p. machine mounted on a "jeep" and fitted with a drag-sheet 4 × 8 metres, as in a previous set of experiments (Talhouk, 1951). The rate of application was determined by the speed of the "jeep", and the setting of the dust flow regulator (hereafter termed "setting") on the duster.

The bottom of the hopper on the duster has a screen flow regulator containing 15 holes, the diameter of each hole being 15 mm. with about 25 mm. between holes. There is a hand lever on the outside of the hopper that moves over 9 positions (settings) numbered 1 to 9. The motion of the lever causes a blade to slide underneath the 15 holes in the screen, shutting or opening them as the case may be. The first three positions open (or close) the first five holes; the next three operate the next five and last three positions operate the last five holes. Setting or position No. 1 opens half of the area of the first 5 holes; setting No. 2 opens 3/4 of the first 5 holes; No. 3 opens all the area of the first five holes. The remaining ten holes will remain closed if settings beyond No. 3 are not used.

---

* Now instructor in Applied Entomology in the School of Agriculture at the American University of Beirut, Lebanon.

It was found that if the "jeep" travelled at 4 km. per hour and the setting was at No. 1, the rate of application would be very nearly 20 kg. of the dust per hectare, and that if it travelled at the same rate but with the setting changed to No. 3, it would be very nearly 40 kg. per hectare. When setting No. 1 was used, and the speed of the "jeep" was raised to 8 km. per hour the application was at the rate of 10 kg. of the dust per hectare.

In order to allow the driver to change speed and the operator on the dusting machine to change the number of the setting, plots A, B and C were separated from each other by a width of 25 metres, marked by flags; these strips were not dusted. The swathe of the drag-sheet was 4 metres and consequently six runs had to be made in each plot to cover its whole area. Care was taken to conduct the experiments under windless conditions so as to minimise drift as far as possible.

The results of the dusting were assessed at 60 and 70 hours after dusting, by counting the number of *E. integriceps* caught in 100 sweeps per plot at each time, using a sweeping net 45 cm. in diameter, fitted with a handle 175 cm. long. All sweeps were made by the same person. Ten sweeps are termed one "count" and ten "counts" were therefore made per plot at each time, the operator moving in a zig-zag manner over each plot. The whole surface of the control plot was covered by sweeps during the first and second assessments. The results are shown in Table I.

TABLE I.

Effect of application of parathion dust at different rates.

Plot	Rate per hectare		Number, and stages of *E. integriceps* caught					Total	Reduction per cent. after treatment
			I	II	III	IV	adult		
A	40 kg.	1st*	0	0	0	1	0		
		2nd	0	0	0	1	0	2	98·4
			0	0	0	2	0		
B	20 kg.	1st	0	1	8	2	0		
		2nd	0	0	6	5	0	22	83·0
			0	1	14	7	0		
C	10 kg.	1st	0	3	16	6	0		
		2nd	0	2	9	7	1	44	65·0
			0	5	25	13	1		
D	0 kg.	1st	1	11	41	9	0		
		2nd	0	4	38	20	1	125	—
			1	15	79	29	1		

* 1st assessment 60 hours after application of the dust.
2nd ,, 70 ,, ,, ,, ,, ,, ,, .

The figures for plot D in Table I show that the majority of the insects were in the first three nymphal stages. The figures also show that, when the majority of the insects are in these earlier nymphal stages and a 0·75 per cent. parathion dust applied at the rate of 40 kg. per hectare, 98·4 per cent. of the insects were killed, and that at the rates of 20 and 10 kg. per hectare, 83 and 65 per cent. kill was obtained, respectively, when compared with the untreated plot.

The effect of the rate of application on the different instars.

Table I also shows the effect of the different rates of application of parathion dust on the younger nymphal stages of this insect. These instars were absent in plot A after it had been treated at 40 kg. per hectare but, as the rate of application was reduced, the number of individuals increased correspondingly.

It is important to bear in mind that when the results of this experiment were assessed, the great majority of the insects were still in their nymphal stages, and, therefore could not fly from field to field. As no barley was planted in this area no infiltration of *E. integriceps* could take place from adjacent fields, to affect the results.†

Another set of experiments was conducted in a different locality on the 16th May 1951 in which a 0·75 or a 0·80 per cent. parathion dust was applied at a rate of 30, 40 and 50 kg. per hectare. The results of these trials could not be assessed properly as a wind blew day and night and prevented accurate counts being made before the wheat had to be cut. Under such weather conditions, the bugs seek shelter between wheat stalks, thus rendering the results of the sweeping inaccurate. After harvesting, however, the soil surface in all the treated plots was found to be covered with the dead insects. The effect of the dust was still pronounced, five days after application, in the plot that was treated at the rate of 50 kg. per hectare and several individuals were found struggling on their backs. Observations were not possible on the other plots due to lack of time.

Trials in 1953.

Cage tests.

Cage tests had to be performed simultaneously with the field test in order to convince farmers in the neighbourhood of the possibility of chemical control of the pest. The results are included here for comparison with those obtained with parathion dusts in 1950 (Talhouk, 1951). In a cage which measured 55 × 30 × 30 cm., 1,406 specimens were introduced and it was placed in plot " A " (see below) and dusted with 0·80 per cent. parathion at the rate of 35 kg. per hectare. Another cage 30 × 30 × 30 cm. containing 234 specimens was left in plot " I ", without treatment, for comparison. Practically all the specimens were adult but there were a few stage IV nymphs. In the first cage, 3¼ hours after treatment, all the 1,406 specimens were paralysed, and in 6¾ hours they were all dead. In the control cage, only two specimens were found dead 24 hours after treatment. To judge whether they were dead or paralysed, the insects were exposed to the direct rays of the sun for five minutes; if they then showed any movement of their appendages, but were unable to walk, they were termed " paralysed "; if they could walk they were counted as " living "; if they could not move any appendage after five minutes' exposure to the sun, they were termed " dead ". No specimen could be considered as " paralysed " in the control cage.

Field experiments.

Field experiments were continued in 1953 on a larger scale than in previous years. They were conducted in the plateau north-east of Idlib, about 350 m.

---

† The alternating of fields of wheat and barley often practised in some parts of Syria creates a serious problem for the wheat as barley matures about 3 weeks earlier. When the barley is cut, the majority of the insects would be in the IVth nymphal instar or even the adult stage. With nothing left to feed on, they would migrate to the nearest wheat, which would be by then in the " milk " stage, and consequently raise the level of infestation of it considerably.

above sea level, an area that is usually moderately to severely infested every year. Plots of wheat and barley are intermixed in the region due to the communal land-ownership system still in use in this part of Syria. The arrangement of the plots chosen for the experiment is shown in fig. 2.

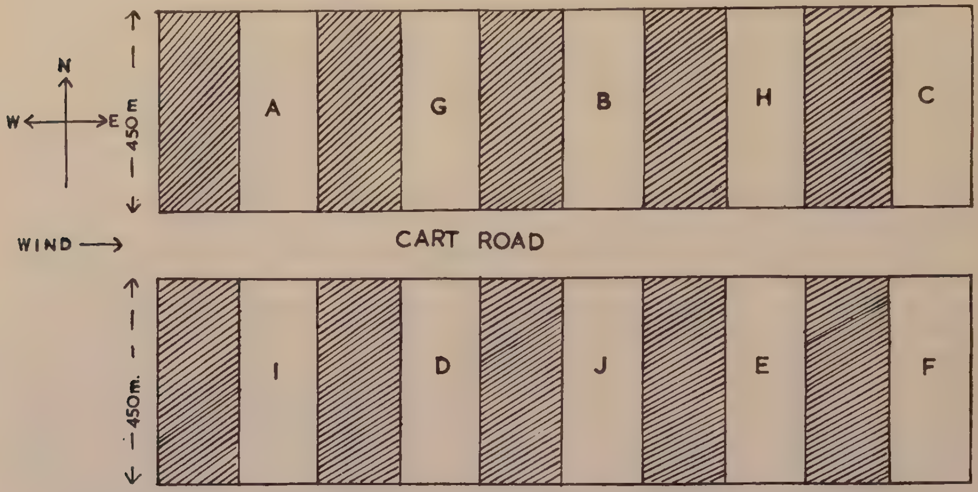


Fig. 2.—Lay-out of 1953 trials with parathion 0·8% dust. Treated plots: A, B, C, D, E. Control plots: F, G, H, I, J. Intervening plots of barley are hatched.

Five plots of wheat were dusted with 0·8 per cent. parathion dust at the rate of 35 kg. per hectare. All the plots were of uniform length, 450 m., but the width varied from 350 to 425 m. Dusting was carried out with a power duster of the " whirlwind " type mounted on a " jeep " but not fitted with a drag-sheet, so as to enable larger areas to be treated on each run; in the 1950 and 1951 trials the field had to be traversed every four metres. The dust was applied by driving through the plots at right angles to the direction of the wind, and at intervals of 15 to 20 metres, depending on the force of the wind. This meant that every plot had to be traversed in a north to south direction about 20 times depending on the condition of the wind. Throughout the experiments the wind blew consistently from west to east, the prevailing direction of the wind during the spring in this part of Syria.

These trials were conducted on the 31st May 1953. Plots A and B were treated early in the morning when no wind was blowing, and the dust settled gently over the plots. Plot C was dusted under slightly less favourable wind conditions. Plots D and E were treated later in the day when an appreciable wind was blowing and about 20 per cent. of the dust rose in a cloud and became dispersed.

The effect of the wind on the efficiency of the dusting is reflected in the number of insects caught 72–74 hours after treatment in 100 sweeps in the different plots. A perimeter of 35 to 40 metres was left around each plot, in which no sweeps were taken, in order to minimise the influence on the final results * of migration of bugs from the harvested barley to the wheat fields. The results are shown in Table II.

It is seen in Table II that the number of insects caught in different " counts " in plots D and E, differed widely. For example in plot E, no insects were recorded in " count " no. 2, and 22 insects in " count " no. 7. Plots A and B

---

* At the time these trials were made, the barley fields were being harvested in this locality.

that were dusted during calm weather, showed more uniformity in the number of insects caught per " count ", the minimum being zero and the maximum 5 or 6. On the other hand, the numbers caught in the untreated plots showed much more regularity.

TABLE II.

Effect of 0·8 per cent. parathion dust, 72–74 hours after dusting.

" Count " no.	Number of live insects taken									
	Treated plots					Untreated plots				
	A	B	C	D	E	F	G	H	I	J
1	0	5	0	4	11	9	13	8	9	16
2	1	3	3	5	0	16	9	16	7	12
3	6	0	5	14	2	12	21	10	2	12
4	5	0	7	2	5	13	9	28	10	21
5	0	0	10	2	7	11	14	21	6	14
6	0	0	0	3	2	13	13	11	14	14
7	0	3	3	13	22	17	16	14	12	9
8	1	0	0	10	3	19	12	19	22	10
9	0	0	0	3	5	16	15	8	6	4
10	1	3	4	2	6	4	9	24	8	11
Total ..	14	14	32	58	63	130	131	159	96	123
Grand total ..			181					639		
Ratio ; treated : untreated = 0·283 : 1										

Taking the averages of the numbers caught in 500 sweeps, the ratio of the treated to the untreated plots is 0·283 : 1 or 71·7 per cent. control. But if the average of plots A and B (dusted under calm wind conditions) alone is compared with that of the untreated plots, then the ratio would be 0·109 : 1, or 89·1 per cent. control.

When these trials were carried out, all the individuals of *E. integriceps* were either fourth-instar nymphs or adults. The majority were adults; nevertheless 35 kg. of a 0·8 per cent. parathion dust per hectare proved highly effective even against these more resistant stages. Unlike the field trials conducted in 1951 (p. 497), very few dead *Eurygaster* were found lying on the surface of the soil in the treated plots on this occasion; this was probably due to the large number of cracks in the soil in this area, which contains a good deal of clay, while the soils of the 1951 trials were mostly sandy loams or alluvial, with no cracks. It is a well-known fact that *E. integriceps*, in all its stages, tends to hide in the soil during the heat of the day (Balachowsky & Mesnil, 1935); therefore it is very likely that many individuals, having been in contact with the dust, would have retired into the cracks to shelter during the day, and were unable to regain the surface of the soil.

Discussion.

The data obtained from field trials conducted in 1950, (Talhouk, 1951), 1951 and 1953, indicate that a 0·75–0·8 per cent. parathion dust applied at the rate of 35 kg. per hectare, during calm weather will reduce infestation of *E. integriceps* in wheat fields by from 70–90 per cent. in its most resistant stages, and that it is even more effective if dusted when the insects are in their younger stages. The best time of application is when the majority are in the second nymphal stage; this will ensure that all the eggs have hatched and, as the insects are at a very vulnerable stage, the insecticide will exert maximum control before it has had time for any appreciable reduction in toxicity to set in (Fahey, Hamilton & Rings, 1952).

Summary.

Experiments were carried out in Syria with parathion dusts for the control of *Eurygaster integriceps* Put. on wheat to ascertain the best time to apply the dust and the most suitable rate of application using a 6 h.p. dusting machine mounted on a "jeep".

A field experiment is described in which a dust containing 0·75 per cent. parathion was applied under a drag-sheet to three plots of wheat at rates of 40, 20 and 10 kg. per hectare, respectively. The insects on the wheat were mostly in the first three instars and the population was assessed by making 100 hand sweeps with a net at both 60 hours and 70 hours after treatment on each plot. The effect of treatment when compared with a control plot was to reduce the insect population in the three plots by 98·4 per cent., 83 per cent. and 65 per cent., respectively.

A further field experiment on a larger scale was carried out in an area in which plots of wheat were interplanted with plots of barley. In this case, the great majority of the insects were fourth-stage nymphs or adults. Five plots of wheat were treated with a dust containing 0·8 per cent. parathion at a rate of 35 kg. per hectare without using a drag-sheet. In two of the plots which were dusted in calm weather, about 89 per cent. control was obtained, in the other plots the effectiveness of the dusting was appreciably reduced by wind.

A cage containing 1,406 live specimens was placed, prior to dusting, in one of the plots of the latter experiment (dusted under calm conditions) and 6¾ hours after treatment all were dead. In the control only two specimens out of a total of 239 originally caged were found dead 24 hours later.

Acknowledgements.

The author wishes to express his sincere thanks again to Mr. G. E. Jones of Plant Protection, Ltd., Fernhurst, England, for assisting him in the first set of trials conducted in 1951.

References.

Balachowsky, A. & Mesnil, L. (1935). Les insectes nuisibles aux plantes cultivées, **1**, p. 1094. Paris, Busson.

Fahey, J. E., Hamilton, D. W. & Rings, R. W. (1952). Longevity of parathion and related insecticides in spray residues.—J. econ. Ent., **45**, pp. 700–703.

Talhouk, A. S. (1951). The effect of parathion dusts on *Eurygaster integriceps* Put. (Hem.).—Bull. ent. Res., **42**, pp. 375–377.

NOTES ON THE DISCOVERY AND BIOLOGY OF *GLOSSINA BREVIPALPIS* NEWST. IN THE MOSSO REGION (URUNDI).

By L. Van den Berghe and F. L. Lambrecht. L.L.

Institut pour la Recherche Scientifique en Afrique Centrale (I.R.S.A.C.); Centre de Recherche Scientifique du Kivu, Bukavu, Congo Belge.

(Plates XXXVI and XXXVII.)

In the course of research on tsetse flies and trypanosomiasis in the Mosso region (Urundi) along the upper Malagarasi river (Van den Berghe & Lambrecht, 1952) we have discovered *Glossina brevipalpis* Newst., a species not previously recorded from Ruanda-Urundi. For this reason, and because relatively little is known about the biology of this species, we think it useful to publish this preliminary note.

The Mosso region lies in south-eastern Urundi. It consists of a large valley extending in a general north–south direction along the rivers Malagarasi and Lumpungu and bounded on the west by a mountain range about 6,000 feet high. The altitude of the bottom of the valley is about 3,700 feet. During investigations in the southern part of this valley, *G. brevipalpis* was encountered in the riverine forest of the upper Malagarasi river (Pl. XXXVI, fig. 1), which at this point forms the border between Urundi and Tanganyika Territory. From here, dense savannah woodland spreads westward towards the mountain range, some fifteen miles away. This typical *Isoberlinia-Brachystegia* woodland is the hunting ground of a *G. morsitans* Westw. population, for which the shady riverine vegetation of the Malagarasi river forms a dry season retreat. *G. brevipalpis*, however, is confined to the dense forest gallery, and only once, during the late rainy season, did we find a female of *G. brevipalpis* far away from this habitat.

Breeding Places.

The evergreen riverine forest along the Malagarasi river is not wide but is rather dense in some places. Seasonal floods occur where the banks are low, and secondary riverine vegetation (Pl. XXXVI, fig. 3) has been formed on the fringe of those parts which are inundated. Although this riverine thicket stretches for many miles along the river, it is infested with *G. brevipalpis* in only a few places. The fly appears to have a preference for those places where the primary and secondary riverine vegetation meet, possibly because of the density of the vegetation at those points and its suitability for breeding (being well above high-water level in the rainy season), or because of the presence of preferred host-animals. This thicket is visited by hippopotami, wild pigs, crocodiles and monkeys (mainly baboons), while in the woodland to the west, many kinds of antelopes and even lions are found.

In the rainy season this thicket failed to produce puparia, but in the dry season many puparia were collected (Pl. XXXVII, figs. 1, 2, 4) at the bases of trees adjoining an evergreen forest "island" which surrounded a spring of clear water. This place was about 200 yards from the secondary riverine thicket and on the day it was discovered it yielded 129 puparia. Puparia of both *morsitans* and *brevipalpis*, sometimes with three other kinds of insect pupae, were often found together. The puparia were found at a depth of about one inch in a mixture of loose soil and humus. These places were usually not heavily shaded. Most breeding places were found at the base of *Brachystegia* trees (Pl. XXXVII, fig. 3). No puparia were found in the dense forest " island ", probably because of its very heavy shade and the amount of soil-water. The *brevipalpis* puparia collected hatched readily after being placed in small containers which were then put into cubical breeding boxes, with 17-inch sides, covered with wire-gauze. Puparia obtained from larvae deposited by wild flies in our field laboratory hatched in about 54 days.

Behaviour.

G. brevipalpis is a crepuscular species. The male is encountered between 17 and 18.30 hours on paths either inside the riverine forest or at the edge of it. Never did we find females under the same circumstances. Indeed it took us quite a while to find any females anywhere. As one walks along the paths towards sunset, a number of males of *G. brevipalpis* will be seen resting on the ground. Disturbed by the stroller, the fly will take off only to return immediately to the path, without making an attempt to attack. Geigy (1950) states that the attraction for the male of *G. brevipalpis* towards the paths is due to phototropism, the paths being much lighter in colour than the dark background of the forest. This appeared to be a valid explanation, but when an army signal panel, made of a plastic material, one side white and the other orange, was placed on the path in such a way that about two square feet of each colour showed, the flies when " driven " towards the panel consented to settle only on the five-inch khaki edge, and every time they were chased about they returned only to this edge. When the panel was hung on the lower branch of a tree, thus disclosing the whole of the orange surface to one side and of the white surface to the other no flies settled on either side. The large, bright-coloured panel should have been strongly attractive if phototropism were the reason for the behaviour of the males of *G. brevipalpis*, and yet no fly ever settled down on it. Since the dark khaki edge is made of cotton and is therefore much warmer than the plastic panel, one is led to believe that the fly is attracted by warmth rather than by colour. If the behaviour of *G. brevipalpis* is thermotropic then the fly might be expected to settle on the paths which have been warmed by the sun all day. It is also possible that the habit of settling on paths towards sunset is being induced by feeding habits. Other tsetse flies (*G. morsitans*) have been seen concentrating on game paths.

While making observations, one evening, we noticed that most of the flies landed face towards the sun, then turned about, head away from the light. These landings and turns-about were observed again and again, each time the fly was disturbed. On a path running parallel with the sunset, the fly landed facing either north or south but never across the path.

Undisturbed, *G. brevipalpis* remains for about one minute in the same place, then flies off and lands again not far from its original resting place. If the hand is carefully advanced towards it, the fly allows approach to within half an inch from its head before it flies away.

It has not been easy to discover the resting places of the female, or even those of the male, during daylight. We finally found them on tree trunks and lower branches in the secondary thicket vegetation of the Malagarasi river. The average height at which they rest is from six to twelve feet above the ground, but one female was captured at the height of only one foot. Male captures are still in excess of female captures, but everything points towards the fact that this thicket forms the true habitat of the species in this region. Males and females generally rest with the head pointed downwards, the abdomen nearer the tree trunk than the head, which is pushed upward by the forelegs (see Pl. XXXVI, figs. 2 & 4).

Table I shows the results of a fortnight's catch of *G. brevipalpis* during daytime:

TABLE I.

Distribution of captures of *G. brevipalpis.*

	♂	♀	Total
Branches and trunks of trees ..	215	32	247
Grass	133	0	133
Tree holes	0	1	1
Bird nests	0	1	1
Tree leaves	25	1	26
On the ground	6	0	6
Total captures	379	35	414

We do not know upon what kind of animals the wild fly feeds and it is clear that there is still much to be learned about its biology. Pires (1950), suggests a close correlation between *G. brevipalpis* and the hippopotamus in the valley of the Maputo river, Mozambique, and considers the latter to be the principal host in that region, because when the hippopotami were chased and driven away from a stretch of the river there followed a quick decrease in the density of the fly, to a level incompatible with the survival of the species. However, this is not a direct proof that *G. brevipalpis* feeds solely on hippopotami, although we ourselves have thought of the possibility that *G. brevipalpis* may feed mostly on them, because of their presence in great numbers near the habitat of the fly. It is possible, however, that Pires, by chasing the hippopotami, has also chased other animals living in or near the *G. brevipalpis* fly-belt and on which the fly fed; or perhaps through his numerous fly-catches he may have destroyed the "back-bone" of the fly population, a *brevipalpis* population being probably not very large in certain places.

We have done a number of microscopical examinations of slides of the blood ingested by captured flies and found it to be mammalian. On rare occasions man is bitten, always, it seems, by female flies. In using two batches of hungry flies, one box containing twenty males and the other twenty females, a man's arm was bitten only by two females.

Infections by Trypanosomes.

Records of dissections of *G. brevipalpis* are not numerous, therefore it may be of interest to publish the results of the dissections carried out during our first investigations. The dissections have been made for the proboscis, salivary glands and gut. The results of the dissections of the salivary glands will be discussed in the next paragraph. Table II shows the number of infections found in the proboscis or gut (or both) during a half-year period for the males and a three months' period for the females.

The figures of this Table seem to indicate that the male fly has a higher infection rate in the late dry season (25.vi–20.ix.51) than during the other periods. We have no rates for the female for this late dry-season period. A number of wild *G. brevipalpis* have been allowed to feed on goats, rabbits and guineapigs; none of the animals developed trypanosomes in their blood. Gibbins (1941) fed 823 *G. brevipalpis* on guineapigs without causing an infection. It would be of great interest, of course, to know which are the trypanosomes carried by *brevipalpis*. Further investigations are being carried on.

Having done approximately 700 dissections of salivary glands between July and December 1951, we finally found two cases of infected glands, both in males. Burtt (1942) found 105 salivary-gland infections in 12,550 males (0·84 per cent.) of *G. brevipalpis* near Amani, Tanganyika, and quotes the record of Bruce & others (1915) of one salivary-gland infection in 496 males (0·20 per cent.). These low rates are not only found in *G. brevipalpis*. Duke (1933) wrote: " In an adequate sample of wild flies (*Glossina*) it is rare to find more than one or two per thousand carrying infective forms of the *brucei* group ". Burtt (*loc. cit.*) quotes as two exceptions amongst the 52 published records he examined, those of Whitnall (1934) who found seven *G. brevipalpis* with infected salivary glands out of 1,129 examined (0·62 per cent.) and Brown (1938) who found 66 infected out of 5,771 examined (1·14 per cent.).

TABLE II.

Numbers of *G. brevipalpis* with trypanosome infections in the proboscis or gut, or both.

Date	Males			Females		
	Dissections	Positive	Rate per cent.	Dissections	Positive	Rate per cent.
25.vi. — 26.vii.51 ..	59	7	11·8	—	—	—
22.vii. — 20.ix.51 ..	42	5	11·9	—	—	—
27.ix. — 14.xi.51 ..	150	10	6·6	—	—	—
22.xi. — 8.xii.51 ..	342	15	4·4	35	2	5·7
17.xii. — 5.i.52 ..	156	8	5·1	21	0	0·0
18.i. — 7.ii.52 ..	280	14	5·0	132	17	12·8
Total ..	1,029	59	5·7	188	19	10·1

Apparently, our finding of two infected salivary glands in 700 examined (0·28 per cent.) is about normal. Experiments are in progress to determine the nature of this trypanosome infecting the salivary glands of *G. brevipalpis* in the Mosso region. We do not believe that this trypansome is necessarily a polymorphic one as assumed by Burtt. Its morphology might be completely different from the trypanosomes of the salivary glands in *G. palpalis* (R.-D.) and *G. morsitans*.

Summary.

Glossina brevipalpis Newst. is recorded for the first time in Ruanda-Urundi, where it has been found in the riverine forest of the upper Malagarasi river in the south-east of the territory.

Resting places of both male and female flies have been found to be on tree trunks, between six and twelve feet up, in heavily shaded riverine thickets.

The species is clearly crepuscular. It is suggested that the male's habit of resting on paths toward sunset is due to thermotropism rather than to phototropism, or that it may be related to passage of game.

Numerous puparia have been found in a late-dry-season breeding ground; these have hatched readily.

The animals encountered near the habitat of *G. brevipalpis* are hippopotami, wild pigs, crocodiles, monkeys and antelopes.

Infections by trypanosomes have been found in proboscis, gut and salivary glands, but experiments on transmission of these trypanosomes from the wild flies to goat, guineapig and rabbit have thus far failed. Research is at present

being carried on to determine the nature of the trypanosomes, of which there are probably several.

References.

Brown, A. A. F. (1938). Trypanosomiasis gambiensis: some observations in Uganda, and their bearing on prophylaxis.—J. trop. Med. Hyg., **41**, p. 247.

Bruce, Sir D. & others (1915). Rep. Sleep. Sickn. Comm. roy. Soc., **16**, p. 27.

Burtt, E. (1942). Observations on the high proportion of polymorphic trypanosome infections found in the salivary glands of *Glossina brevipalpis* near Amani, Tanganyika Territory, with a note on the appearance of the infected glands.—Ann. trop. Med. Parasit., **36**, pp. 170–176.

Duke, H. L. (1933). Studies on the factors that may influence the transmission of the polymorphic trypanosomes by tsetse. I. A review of existing knowledge on this subject, with some general observations.—Ann. trop. Med. Parasit., **27**, pp. 99–118.

Geigy, R. (1950). Observations sur quelques espèces de *Glossines* de l'Afrique centrale.—Congr. Internat. Hyg. & Méd. Méditerr., Alger 1950.

Gibbins, E. G. (1941). Studies on the bionomics, control and natural infectivity of the riverine *Glossina palpalis* subspecies *fuscipes* Newstead in the West Nile District of Uganda.—Ann. trop. Med. Parasit., **35**, pp. 195–218.

Pires, F. A. (1950). A control of the *G. brevipalpis* Newst., in the valley of the Maputo River.—Bur. perm. interafr. Tsé-tsé Tryp., no. 143.

Van den Berghe, L. & Lambrecht, F. (1952). *Glossina morsitans* e a tripanosomiase em Mosso-Sul (Urundi).—I. Congr. Nac. Med. Trop., Lisbon, 1952.

Whitnall, A. B. M. (1934). The trypanosome infections of *Glossina pallidipes* in the Game Reserve, Zululand. (Final report.)—Onderstepoort J. vet. Sci., **2**, pp. 7–21.

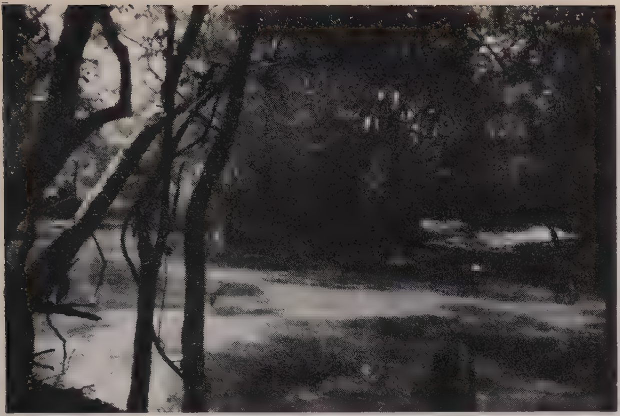


FIG. 1. The upper Malagarasi river and its riverine forest. Dry season, July 1951.

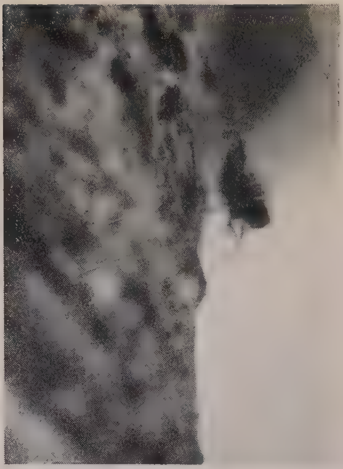


FIG. 2. Close-up photograph of *G. brevipalpis* resting on a tree.

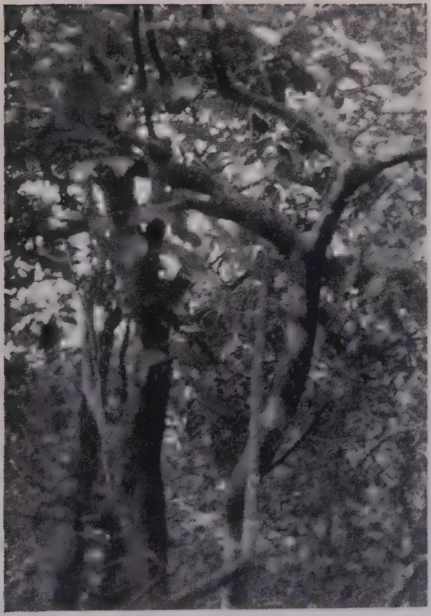


FIG. 3. The vegetation of the secondary riverine thicket; habitat of *G. brevipalpis*.

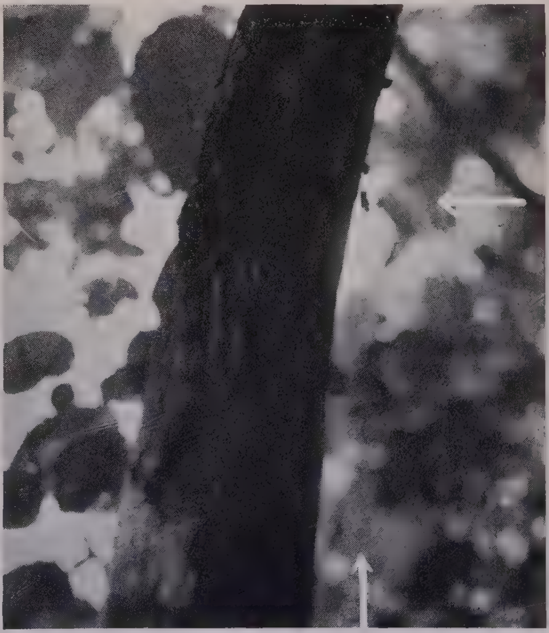


FIG. 4. *G. brevipalpis* resting on a tree trunk. Note typical position; head down and pushed away from the trunk.

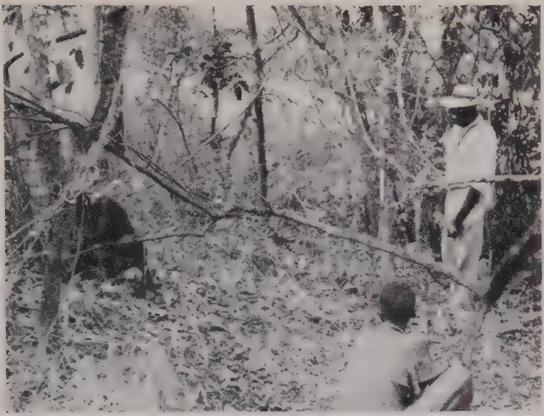


FIG. 1. Site (adjoining the heavily shaded forest island) where puparia of *G. brevipalpis* and *G. morsitans* were found in the late dry season.

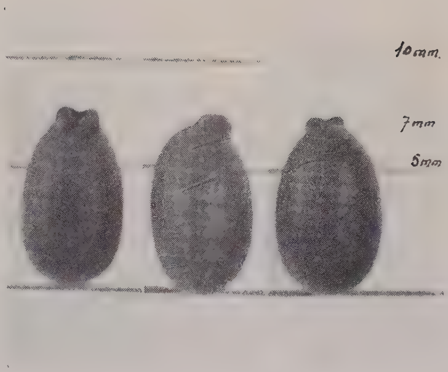


FIG. 2. Puparia of *G. brevipalpis*, front, side and back.

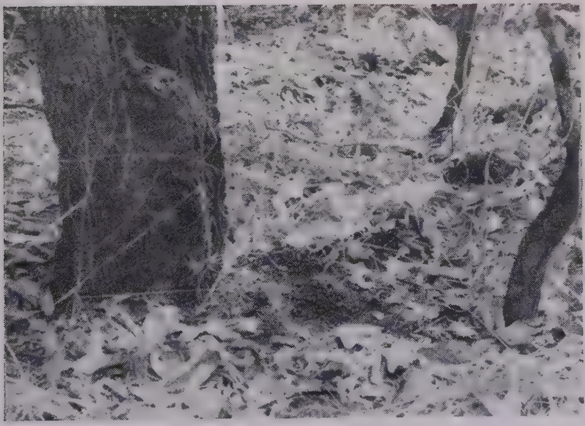


FIG. 3. Base of *Brachystegia* tree where puparia have been unearthed.

FIG. 4. Close-up view of a freshly unearthed puparium.

THE EFFECTS OF ATMOSPHERIC PRESSURE ON THE FLIGHT RESPONSES OF *AËDES AEGYPTI* (L.).*

よし.

By W. O. Haufe.

Department of Zoology, University of Western Ontario, London, Ontario, Canada.

A comprehensive review of the existing literature on the effects of variations in atmospheric pressure on insect behaviour has been published by Wellington (1946*a*). The views of the authors whom he cited are for the most part contradictory, although there are many instances of increased flight activity during periods of falling pressure. It is well known that insects can withstand extreme changes of pressure without any fatal or even damaging effects on their physiology as reported by Back & Cotton (1925), Cleveland (1925), Cole (1906), Greenwood (1906), Huber (1814), Lutz (1929), Roller (1906), Wellington (1946*b*). Experiments with extreme variations of pressure have possibly little relation to the actual conditions in the atmosphere. Therefore, it is desirable to determine whether small variations in pressure approaching the order of natural variations in the atmosphere have any effect on the flight activity of mosquitos.

Of the few species of mosquitos that can be reared satisfactorily in the laboratory, *Aëdes aegypti* (L.) lends itself best to this type of problem. It is easily reared, survives handling well under laboratory conditions, and is normally active over a range of combinations of environmental factors that can be maintained readily during laboratory experiments.

The experiments herein described investigated the effects of individual factorial components of atmospheric pressure on the number of times individuals in a group of mosquitos became airborne in a given period. There are four possible factorial components in changing atmospheric pressure that may be significant in producing a response in an insect. These are level (*per se*) of pressure, direction of pressure change, amount of pressure change, and rate of pressure change.

Method and Materials.

Apparatus.

Five-gallon carboys with suitable connections to manometer tubes served as pressure chambers. Soft rubber stoppers of proper size and bored for air-line connections proved to be airtight over extensive periods of time. A vacuum pump was used to provide the pressures below atmospheric pressure while the laboratory air-line provided those above atmospheric pressure. In the laboratory experiments with *A. aegypti*, an arrangement similar to fig. 1 was used. In every experiment, temperature control was well within the range of 80 ± 2 degrees F. In subsequent experiments in a field laboratory, the degree of control over the environmental air pressure of experimental mosquitos was improved by immersing the chambers in constant-temperature water baths. When properly adjusted, four pinchcocks, placed as shown in fig. 1, equalised the rate of increase and decrease of pressure in the two pressure chambers during experiments involving simultaneous observations. For convenience in observing the flights of mosquitos, the half of each chamber distal to the observer was covered with a white screen. Shaded lamps arranged to illuminate the chambers equally from the immediate front allowed the observers to remain in the shadow.

---

* This paper is a summary of a thesis submitted in partial fulfilment of the requirements for the M.Sc. degree.

Method.

Single pressure chambers were used for a preliminary study of variability in population behaviour; but in the remainder of the investigation two groups of mosquitos of approximately the same age were confined in separate pressure chambers. Temperature variations during any single experiment were not more than ± 1 degree F. The relative humidity was kept in excess of 80 per cent. by saturating air at 85°F. with moist absorbent cotton; when the temperature was returned to 80°F. the appearance of a slight condensation indicated the air to be saturated or nearly so. Preliminary checks on saturation deficiencies for various experimental conditions were made with an atmometer inside the chamber. The number of pressure changes in any single experiment was limited by the requirement that no group of mosquitos should be subjected to a drop of more than 20 per cent. of the assumed initial 100 per cent. R. H. during the observations. The number of "take-offs" from a resting position on the surface of the chamber was used as an index of activity in all experiments. Where two or more groups of mosquitos were used, counts of flights were made simultaneously by two observers who alternated for two different experiments with the same pressure conditions and with the same mosquitos.

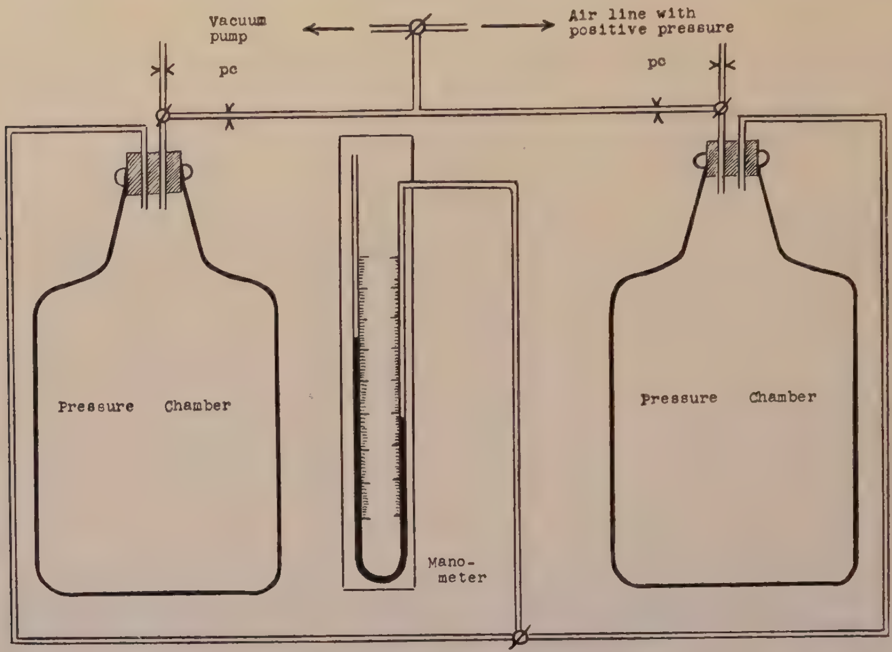


Fig. 1.—General arrangement of pressure chambers and connecting air-lines used in experiments. (pc = pinchcocks.)

The possibility of the acclimatisation of experimental mosquitos was considered in all experiments. A standard time procedure was followed to permit uniform acclimatisation of mosquitos in experiments where two or more experimental groups were involved or when the behaviour of a single group was compared during different periods. Each group of mosquitos was allowed a period of six hours to acclimatise itself to the initial pressure conditions preceding the experiment. At the end of the six-hour period, the pressure changes were performed and the cumulative numbers of "take-offs" were recorded for an observation-period during or after the change.

Experimental material.

Adult female mosquitos were obtained from the stock of *A. aegypti* maintained by the Department of Zoology, University of Western Ontario. Periodically, pupae were collected from common rearing stock and placed in a small cage prior to emergence. Since the mosquitos were not fed, the males died quickly under normal laboratory conditions to leave a pure stock of females. Selection of adult mosquitos from this stock four days after the peak emergence usually yielded only female mosquitos, which could be moved directly to the pressure chambers with a minimum of handling and physical damage. Mosquitos were not subjected to more than one experiment except in the investigation of variability and acclimatisation in flight behaviour.

Observations and Results.

Variability.

Some measure of the degree of reproducibility of behaviour in various stocks of experimental mosquitos was necessary for a reasonably accurate estimation of those differences in flight activity caused strictly by pressure conditions. The standard procedure for this type of investigation involved a single group of thirty female mosquitos. The mosquitos were placed in a chamber which was evacuated to a pressure of 675 mm. of mercury. After a lapse of six hours, the following sequence of pressure changes and recording periods was performed: (1) evacuation to 650 mm. at a uniform rate of 1 mm./sec.; (2) number of " take-offs " recorded for a 15-minute period immediately following pressure change; (3) mosquitos allowed to rest for two hours; (4) pressure raised to 675 mm. at the same uniform rate (1 mm./sec.); (5) number of " take-offs " recorded for a 15-minute period immediately following pressure change; (6) mosquitos allowed to rest for two hours; (7) evacuation to 650 mm. at the same uniform rate; (8) number of " take-offs " recorded for a 15-minute period following pressure change; (9) mosquitos allowed to rest for two hours; (10) pressure raised to 675 mm. at the same uniform rate; (11) number of " take-offs " recorded for a 15-minute period following the pressure change. This sequence of fluctuations of pressure and 15-minute recordings of " take-offs " provided four values for the flight activity—two following a rising pressure and two following a falling pressure. These values are shown in Series A of Table I. Conditions of the experiments were equal for temperature, saturation deficiency, light, and rate of change of pressure which was 1 mm. per second.

To eliminate the influence of the initial starting pressure on the flight activity resulting from the pressure fluctuations described, the whole sequence was repeated with the same group of mosquitos. This time, the mosquitos were subjected to the six-hour acclimatisation period at a pressure of 650 mm. (the opposite extreme of the range of fluctuation); the sequence of pressure fluctuations and 15-minute recordings of " take-offs " was performed in the reverse order to supply four more values for flight activity—two following a rising pressure and two following a falling pressure. These values are shown in Series B of Table I. — ?

The values for the flight activity for periods following a rising pressure (a) as opposed to those for periods following a falling pressure (b) were combined, including those of both Series A and B, and plotted in fig. 2. The range of the deviations of individual values is represented by the hatched areas enclosing the two lines.

The direct investigation of variability of flight behaviour included two stock groups of mosquitos. These two groups were (i) adult female mosquitos of mixed parentage, 4 days old, and derived from larvae hatched from eggs on the same day, and (ii) adult female mosquitos of mixed parentage, 5½ days old, and of the same developmental history as (i). The data from this investigation were

TABLE I.

Number of flights of mosquitos recorded on a cumulative basis following rising pressures from 650 to 675 mm. and falling pressures from 675 to 650 mm.

Pressure	Sequence of pressure fluctuations	Temperature (degrees F.)	Series	Accumulation of flights with minutes														
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Rising to 675 mm. (a)	1	79—81	A	22	38	49	62	82	101	131	162	192	221	236	261	284	309	341
	3	79—81	A	36	69	94	120	144	159	176	192	217	240	265	287	305	317	339
	6	79—81	B	23	43	64	83	100	113	138	163	179	193	210	231	254	280	302
	8	79—81	B	26	40	55	76	101	115	129	145	164	185	197	204	226	249	275
Falling to 650 mm. (b)	2	79—81	A	26	32	37	51	70	87	97	110	131	151	174	192	212	224	239
	4	79—81	A	24	43	57	66	82	93	103	116	132	154	173	185	207	224	23
	5	79—81	B	29	39	54	67	87	102	116	135	151	166	180	193	204	220	221
	7	79—81	B	26	40	50	63	74	89	107	122	129	143	154	171	185	191	194

No. of mosquitos = 30 per group. Age of mosquitos = 4 days.
Stock derived from larvae hatched same day from eggs of different parentage.

supplemented by data on a third group obtained indirectly from another series of experiments performed over a period of several months, namely, adult female mosquitos of mixed parentage, 4 days old, and hatched from eggs during widely separated periods of time.

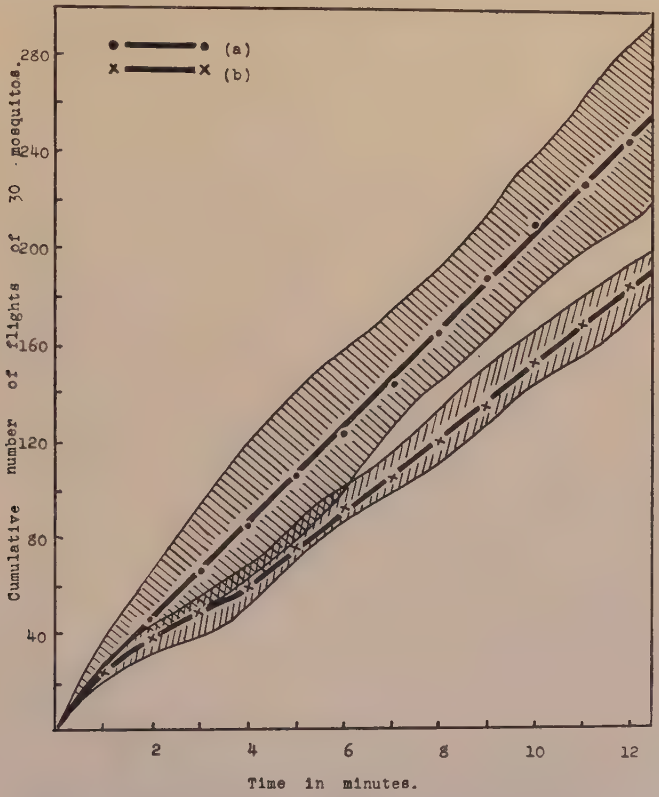


Fig. 2.—Graphs showing cumulatively the flight activity of 30 mosquitos, (a) after the pressure was raised from 650 mm. to 675 mm. and (b) after the pressure had fallen from 675 mm. to 650 mm. Hatching represents the maximum variation of values.

The coefficients of variability were calculated for the flight activity of the three groups of experimental stock mentioned above. These values are tabulated in Table II. In the comparison of mosquitos with similar developmental histories, *i.e.*, emerging within an eight-hour period of stable pressure from the same brood, the coefficient of variability of flight activity was 9·5 at 4 days following emergence as compared to 15·8 at 5·5 days. In the comparison of mosquitos at the same age (4 days), the coefficient of variability of flight activity was 31 * among individuals with different developmental histories, *i.e.*, emerging at various times over a six-month period, as compared to 9·5 among individuals restricted in their emergence to the same developmental conditions, *i.e.*, emerging within an eight-hour period in which pressure was stable to within ± 1 mb. The coefficient of

---

* Table II.—Since each average value was derived from 4 separate counting periods, the coefficient of variability of a *single* value of any group for this flight activity of groups of mosquitos with different developmental histories would be calculated to be $15{\cdot}5 \times \sqrt{n/1} = 15{\cdot}5 \times \sqrt{4} = 31$ (approximately).

TABLE II.

Comparison of the variability found in flight behaviour among various mosquitos.

	Stock history (Mosquitos)	Age (adults)	Accuracy of data	Number of mosquitos used	Standard Deviation*		Coefficient of Variability		
					Increased pressure	Decreased pressure	Increased pressure	Decreased pressure	Average
1.	Larvae hatched *same* day from eggs of different parentage	4 days	Counts for single periods	30	31·7	19·6	10·1	8·9	9·5
2.	Larvae hatched *same* day from eggs of different parentage	$5\frac{1}{2}$ days	Counts for single periods	30	10·5	4·35	18·7	12·8	15·8
3.	Larvae hatched *different* days from eggs of different parentage	4 days	Average of counts for single periods	20	25·4	16·2	15·2	15·9	15·5

Calculated average coefficient of variability for the mosquito stock (3) for counts of single periods $= 15{\cdot}5 \times \sqrt{\frac{n}{1}} = 15{\cdot}5 \times \sqrt{\frac{4}{1}} = 31{\cdot}0$ approx.

Standard deviations (*) stated in terms of number of flights in a 15-minute period.

variability of flight activity for mosquitos with different developmental histories was calculated indirectly from a large number of experiments designed to investigate the effects of pressure changes on activity.

Acclimatisation.

The flight behaviour of mosquitos in response to atmospheric pressure was found to be considerably modified by their past experience of this factor. If two mosquitos, one of which has been exposed to a high pressure and one to a low pressure for a considerable length of time, are both subjected to the same pressure somewhere between the two extremes, they will behave differently for the first few hours until they have been acclimatised to the new pressure condition. The following type of experiment was designed to investigate the length of period necessary for complete acclimatisation to pressure conditions.

A neutral pressure level (x), at which the numbers of "take-offs" were recorded, was selected for each experiment. One group of 30 mosquitos in a pressure chamber was exposed to a pressure of (x + a) while a second group of 30 mosquitos in another pressure chamber was exposed to a pressure of (x − a) for an arbitrary period of six hours. At the end of this period the pressure in each of the chambers was raised or lowered, depending on the previous level, to the same neutral level (x). The number of "take-offs" was simultaneously recorded at one-minute intervals for each of the two groups of mosquitos until both groups showed approximately the same level of flight activity.

This procedure was used in several experiments to investigate the acclimatisation of mosquitos to two components of pressure, (i) the direction of the change and (ii) amount of pressure change. For purposes of experiment, acclimatisation to the two components are interdependent in their effects. The acclimatisation to direction of change of pressure was considered to be the reaching of a state of equal activity in the two groups of mosquitos (those that had been subjected to a fall of, say, x mm. and those that had been subjected to a rise of the same amount), *i.e.*, when the factor of direction of change had ceased to give differential activity. Similarly, acclimatisation to the amount of pressure change was considered to be the reaching of a state of equal ratios of activity (the number of "take-offs" for a given fall in pressure as compared to the number for a rise of the same amount) irrespective of the amount of rise or fall of pressure applied to paired groups of mosquitos, *i.e.*, when the factor of amount of change has ceased to give differential ratios. While the type of acclimatisation in (ii) was followed to completion by continuous observations, the same success cannot be reported for type (i); the time necessary for complete acclimatisation in (i) was too great to be followed to the end by continuous observation.

As described in a later section, the greatest differences in flight activity caused by changing pressure occurred when the general pressure level approximated 780 mm. This pressure level was later selected as possibly the best level at which to investigate the acclimatisation of mosquitos to the direction of the pressure change.

One group of 30 mosquitos was placed in a chamber with a pressure of 795 mm. and another group in another chamber with a pressure of 765 mm. After a lapse of six hours at constant temperature, pressure, saturation deficiency and light, the pressure in each chamber was raised or lowered, depending on the original pressure level, to 780 mm. Immediately following the pressure changes, the number of "take-offs" was simultaneously recorded in 2-minute intervals by two observers who recorded the differences in flight activity as continuously as possible. An example of this type of experiment is shown in fig. 3. The difference in the levels of flight activity are clearly defined for the first hour following the completion of the pressure change. Thereafter the flight activity of both groups gradually approaches a mean level as the acclimatisation increases.

Satisfactory observation of mosquito behaviour maintained constantly over a period of time was limited to a maximum of three hours; another type of experiment was designed to discover the length of time necessary for the completion of acclimatisation. It should be noted that a standard time lapse of six hours was arbitrarily selected to precede all experiments to allow for acclimatisation. The following type of experiment was designed to determine the adequacy of this period in the routine of other experiments.

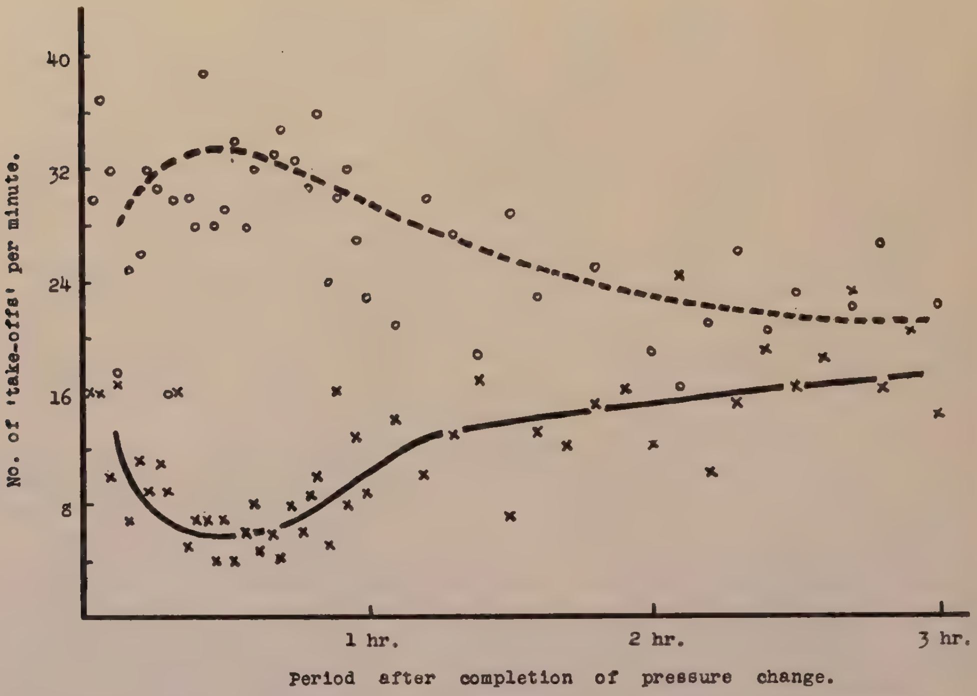


Fig. 3.—Graph showing the increase in acclimatisation of mosquitos over a three-hour period. Circles represent the number of "take-offs" in 2-minute intervals after the pressure had fallen by 15 mm. to the 780 mm. level; crosses represent the number of "take-offs" in 2-minute intervals after the pressure had been raised by 15 mm. to the 780 mm. level.

A series of nine experiments was designed to include six different pressure levels. Each experiment was limited to four pressure levels but values for flight activities for six different levels were obtained by using different combinations of pressures for each experiment in the series as shown in Table III.

In each experiment, four pressure chambers, each containing thirty mosquitos, were used simultaneously. At zero time, each one of four groups of mosquitos was subjected to a different pressure level. Each of the four groups of mosquitos was allowed a six-hour period for an increase of acclimatisation to the new level of pressure under standardised conditions of light, humidity, and temperature. Since this type of experiment was done in a constant temperature and constant humidity room (temperature = 76 ± ·5 degrees F., relative humidity = 80 ± 2 per cent.), a minimum of difficulty was experienced in maintaining pressures constant within the chambers over a six-hour period. At the end of the acclimatisation period, the numbers of "take-offs" during a thirty-minute period were recorded simultaneously for the four groups of mosquitos.

In this investigation, flight activity was found to be random in character after a 6-hour acclimatisation period. The dispersion of the values for flight activity varies from 10 to 23 per cent. of the average for each of the six pressure levels. When tested statistically for correlation with pressure level, these values had a coefficient of correlation of $-0{\cdot}188$ *; this figure included a correction for the small number of classifications of pressure level. The probable error for this correlation was ± 0·212. Since the probable error was greater in magnitude than the coefficient of correlation, there was no statistical correlation between flight activity of the mosquitos and pressure level after a six-hour period of acclimatisation.

TABLE III.

Comparison of the number of flights made by mosquitos following a 6-hour period of acclimatisation at various pressure levels.

No. of exp.	No. of flights (30 mosquitos in 30 min.) at pressure of Hg. of:—					
	800 mm.	750 mm.	700 mm.	650 mm.	600 mm.	550 mm.
1	48	105	58	37		
2		64	89	80	91	
3			66	59	45	32
4	25			78	86	73
5	46	103			65	35
6	41	77	79			55
7	37	101	68	64		
8		83	78		74	37
9	38			71	70	42
Average	39	89	73	65	72	46
Probable error	5·5	11·3	7·5	10·7	11·1	10·6

On the basis of the results of the two types of experiments just described, there is considerable evidence that acclimatisation had an important influence on the flight activity of the mosquitos when response to the direction and amount of pressure change was studied. Although the actual period necessary for this type of acclimatisation was not defined precisely, it was found to be less than six hours and greater than three hours.

---

* Coefficient of correlation $= r = \dfrac{\Sigma x_1 y_1}{\sqrt{\Sigma x_1{}^2 \;.\Sigma y_1{}^2}} = -0{\cdot}479$

Correction of r for 6 sets of data:

$$(r^1)^2 = 1 - \frac{(1 - r^2)\ (n - 1)}{n - 2} = \frac{1 - ({\cdot}2285 \times 5)}{4} = 0{\cdot}0356$$

Therefore correct coefficient of correlation $= r^1 = -{\cdot}188$

$$\text{Probable Error} = \pm\ 0{\cdot}6745\ \frac{(1 - r^2)}{(\sqrt{n})} = \pm\ {\cdot}212$$

Coefficient of correlation (– 0·188) is less than the probable error (± ·212).

The comparative effects of a fall as against a rise in pressure could be expressed as a ratio, f_d/f_i, in which f_d represented the number of flights per minute after the pressure had fallen a given amount at the uniform rate to a given level, and f_i represented the number of flights per minute after the pressure had been raised the same given amount at the same uniform rate to the same given level. The use of this ratio allowed data from different stock groups to be compared without compensation for the high variability observed between individuals emerging under different pressure conditions. It also offered a convenient method of following the progress of acclimatisation, since when f_d/f_i is 1, the acclimatisation is complete. The flight activity expressed by two lines in fig. 3 at a pressure of 780 mm. is expressed as this ratio in a single line as the upper curve in fig. 4. The lower curve expresses similar data obtained at a pressure of 630 mm.

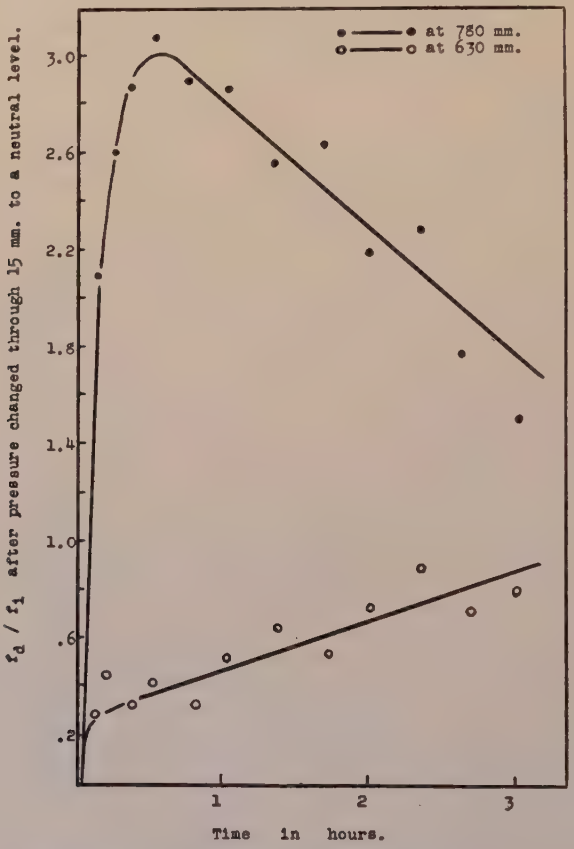


Fig. 4.—Graphs comparing the acclimatisation of mosquitos to a change of pressure at two levels during a three-hour period. When the increase of acclimatisation is complete, $f_d = f_i$ and f_d/f_i approaches unity. (See text.)

To investigate the acclimatisation of mosquitos to the amount of change of pressure, the standard type of experiment described in this section was repeated with various groups of mosquitos over a period of several days at the 630 mm. level. The conditions for all these experiments were the same except that the amount of pressure change was varied from one experiment to the next. All mosquitos used were 4 days old.

The period necessary for the acclimatisation of mosquitos to the amount of change of pressure was found to be approximately 30 minutes. The smoothed curves for experiments using four amounts of pressure change are shown in fig. 5.

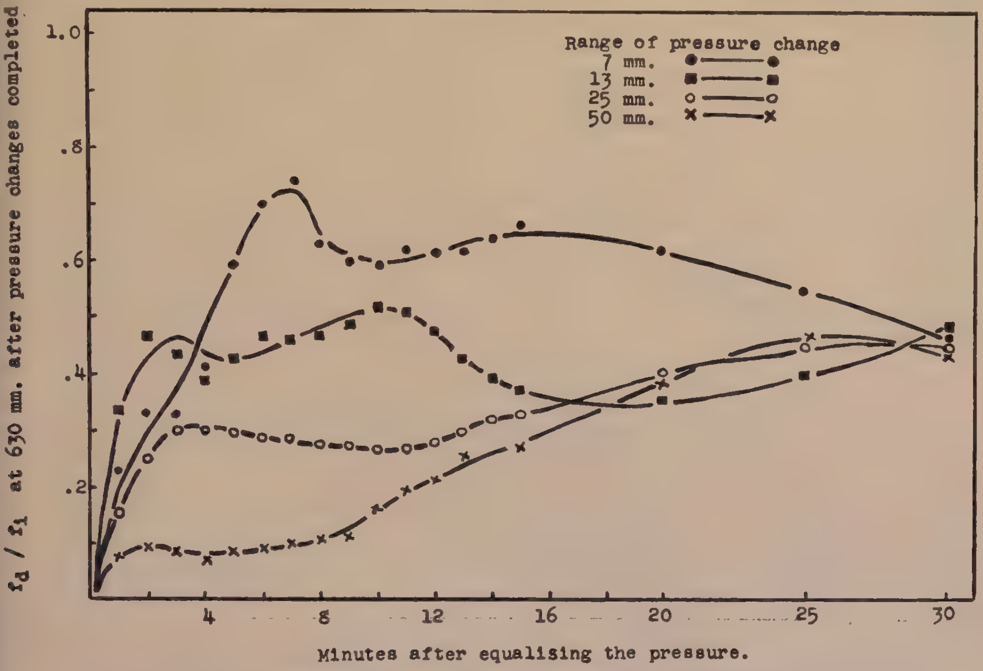


Fig. 5.—The acclimatisation of mosquitos to the same level of pressure (630 mm.) after various amounts of pressure change.

Each curve represents the difference in flight activity between a group of mosquitos for which the pressure had fallen by a given amount and a group of mosquitos for which the pressure had been raised the same amount to the same level. This difference in flight activity was found to be increased as the amount of change of pressure was increased from 7 to 50 mm., *i.e.*, the ratio f_d/f_i fell to a smaller fraction of unity. At the end of a 30-minute period following the pressure changes, the ratio f_d/f_i in all cases had reached a value of 0·4 to 0·5. This may be interpreted as meaning that the acclimatisation to *amount* of pressure change was complete since the ratios approached the same value in this period for all the pressure changes; but the acclimatisation to pressure change in the two directions was unequal since the ratio was still far from unity.

Effect of pressure on flight activity during a pressure change.

When the pressure is varied at a uniform rate over a given range with respect to a normal pressure level, there is a distinct difference in the number of flights of mosquitos during an increasing pressure as compared to the number during a decreasing pressure. Several experiments were performed with different groups of five mosquitos each to show the difference in flight behaviour during rising or falling pressures of a uniform rate.

An arbitrary procedure was adopted for this type of experiment. By trial and error the lowest rate of rising or falling pressure that could be maintained reasonably uniform for the pressure system over a range of 200 mm. was found to be approximately 7·7 mm./min. For each experiment a period of 26 minutes was required for the pressure in the chamber to rise or fall through a range of 200 mm. between the limits of 530 and 730 mm. Five mosquitos were exposed to a constant pressure of 630 mm. in a chamber for six hours to become acclimatised to a pressure which was median for the range of pressure used in the experiment. At the end of the acclimatisation period the pressure was raised to 730 mm. After an interval of 10 minutes the pressure was decreased uniformly for 26 minutes to 530 mm. during which time the cumulative number of "take-offs" was recorded. After a 10-minute interval the pressure was increased uniformly for 26 minutes to 730 mm. during which time the number of "take-offs" was recorded.

The results of a single experiment are shown in Table IV. In a series of six experiments, three of which were started at 530 mm. and three at 730 mm., the numbers of flights while the pressure was falling at 7·7 mm./min. for 26 minutes varied from 0 to 6 as compared to 29 to 51 while the pressure was rising at the same uniform rate for the same length of time.

TABLE IV.

Comparison of the number of flights of mosquitos occurring during rising and falling pressures over the same range.

Time in minutes	Accumulation of flights with time for 5 females during a pressure *increase* of 200 mm. Hg. *to* normal at a rate of 7·7 mm./min.	Accumulation of flights with time for 5 females during a pressure *decrease* of 200 mm. Hg. *from* normal at a rate of 7·7 mm./min.
1	1	0
2	2	0
3	2	0
4	3	0
5	3	0
6	4	0
7	4	0
8	5	0
9	5	0
10	5	0
11	5	0
12	5	0
*13	20	0
14	24	0
**15	30	0
16	32	0
17	32	0
18	34	0
19	35	0
20	35	0
21	37	0
22	37	0
23	39	0
24	41	0
25	50	0
26	51	0

* at 100 mm. below normal pressure.
** at 80 mm. below normal pressure.

Note: The Table represents a single fluctuation of pressure. Pressure range 530 to 730 mm.

Effect of pressure at different levels.

The effect of pressure changes to the amount of 15 mm. and 30 mm., respectively, was investigated at various pressure levels above and below the normal pressure level. For the experiments, neutral pressure levels (x) were selected at appropriate intervals between 530 and 830 mm. One group of 20 mosquitos was placed in a pressure chamber with a pressure of x + 15 mm., while another group of 20 mosquitos from the same brood was placed in another chamber with a pressure of x − 15 mm. (Series A). A similar series of experiments was made with pressures at x + 30 mm. and x − 30 mm. (Series B), and at x + 7 mm. and x − 7 mm. (Series C). An acclimatisation period of six hours was allowed for each experiment with equal conditions of temperature, moisture, and light for both groups of mosquitos. At the end of the acclimatisation period the pressures in the chambers were raised or lowered at 1 mm./sec. to the same neutral level (x). The numbers of " take-offs " (a_1) in each of the two pressure chambers during the following 30 minutes were recorded simultaneously by two observers. The experiment was repeated with the pressure changes reversed in the two chambers, thus obtaining a second pair of figures for " take-offs ", (a_2), which equally contributed to give the average values $\bar{a}$ after a fall and after a rise of pressure, respectively.

The rates of " take-offs " after falling and after rising pressures are tabulated

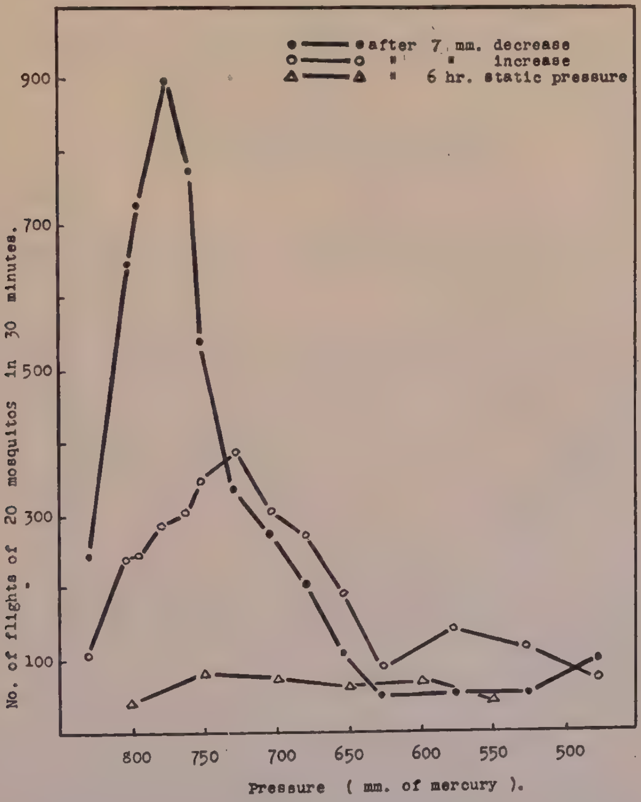


Fig. 6.—Graphs comparing the flight activity of *A. aegypti* during 30 minutes following a six-hour period of acclimatisation at constant pressure with the flight activity during the same period following an increase and a decrease of 7 mm. of pressure.

TABLE V.

A summary of the results of experiments on the effect of rising and falling pressures on the flight activity of mosquitos in relation to level of pressure.

No. of experiment	Series	Neutral pressure level (mm. Hg.)	Range of pressure change (mm. Hg.)	F_d			F_i			$F_{d_{\bar{a}}} / F_{i_{\bar{a}}}$		$F_{d_{\bar{a}}} + F_{i_{\bar{a}}}$	
				a_1	a_2	$\bar{a}$	a_1	a_2	$\bar{a}$	Series A	Series B	Series A	Series B
1	A	830	15	222	186	204	150	108	129	1·58		333	
2	B	830	30	193	131	162	244	164	204		·79		366
3	A	805	15	552	446	499	289	215	252	1·98			
4	A	795	15	712	604	658	327	245	286	2·30			
5	A	780	15	786	724	755	338	286	312	2·42		1067	
6	B	780	30	91	53	72	69	59	64		1·1		136
7	A	765	15	903	821	862	417	311	364	2·37			
8	A	755	15	688	654	671	327	283	305	2·20			
9	A	730	15	293	197	245	352	286	319	·77		564	
10	B	730	30	80	72	76	51	77	64		1·2		140
11	A	705	15	342	282	312	340	362	351	·89			
12	A	680	15	218	248	233	228	326	277	·84		510	
13	B	680	30	62	44	53	183	117	150		·35		203
14	A	655	15	115	71	93	238	184	211	·44			
15	A	630	15	72	74	73	125	185	155	·47		228	
16	B	630	30	29	45	37	96	110	103		·36		140
17	A	580	15	32	16	24	132	94	113	·21		137	
18	B	580	30	50	28	39	145	99	122		·32		161
19	A	530	15	71	49	60	113	159	136	·44		196	
20	B	530	30	29	53	41	114	62	88		·47		129
											*Total	3035	1275

*$F_{d_{\bar{a}}}$ and $F_{i_{\bar{a}}}$ values for Series C following a 7 mm. rise or fall of pressure can be read directly from fig. 6. The total $F_{d_{\bar{a}}} + F_{i_{\bar{a}}}$ for Series C was 3185, a value not significantly different from the total for Series A.

The sum of $F_{d_{\bar{a}}}$ and $F_{i_{\bar{a}}}$ is only shown where comparison is possible between flight activity at the same level of pressure in Series A and Series B.

in Table V (Series A and B) and plotted in fig. 6 (Series C) along with the rates after a six-hour acclimatisation period for comparison. The maximum effects of increasing and of decreasing pressures on flight activity following the completion of the pressure change did not occur at the same pressure level. The maximum number of " take-offs " in a 30-minute period following a 7 mm. fall in pressure was recorded at 780 mm. The maximum number of " take-offs " in the same period following a 7 mm. rise in pressure was recorded at 735 mm. There was little significant difference between the effects of increasing and decreasing pressure on flight activity at pressure levels below 630 mm.

The figures tabulated in Table V were then calculated as the ratio F_d / F_i*, those for 15 mm. and 30 mm. changes of pressure being placed in separate columns. In fig. 7 the values for this ratio are plotted against the neutral pressures concerned. The curve shows that at neutral pressures below 735 mm. this ratio is less than 1; the activity after increasing pressure exceeds that after decreasing pressure. At neutral pressures above 735 mm. the ratio is greater than 1 and reaches a peak of 2·4 at 780 mm. at which the activity after decreasing pressure is 2·4 times that after increasing pressure.

Effect of amount of pressure change.

A comparison of the flight activity following a 30 mm. change in pressure as against a 15 mm. change may be obtained from the total figures of " take-offs ",

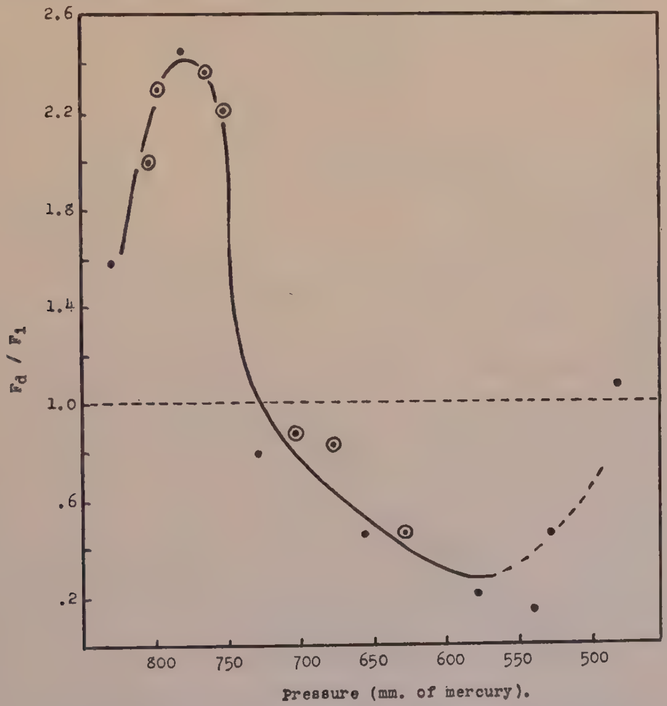


Fig. 7.—The relation of F_d/F_i (the ratio of the number of " take-offs " for falling pressure to the number of " take-offs " for increasing pressure) to level of pressure for the neutral pressure levels investigated between 500 mm. and 800 mm. (See text.)

---

* F_d designates the number of " take-offs " in a 30-minute period; it is to be distinguished from f_d which designates the number of " take-offs " per minute in any given minute.

$F_d + F_i$, for both rising and falling pressures as shown in the last two columns of Table V. The total flight activity for 15 mm. changes of pressure was approximately 2·5 times as great as the total flight activity for 30 mm. changes of pressure at corresponding neutral pressure levels. Experience in other investigations indicated that large changes of pressure had little quantitative effect, if any, on the flight activity of mosquitos. Usually, mosquitos showed little difference in behaviour for either rising or falling pressures when the amount of the pressure change greatly exceeded the normal range of fluctuations of barometric pressures in nature.

Effect of rate of change in pressure.

Although it was impossible to achieve duplication in low, regulated rates of change approaching the order of those pressure changes normally occurring in nature, exploratory experiments were made with rates between 6·4 and 66 mm./min. Counts of "take-offs" were taken during the 10-minute period immediately following the completion of the pressure change.

In each experiment the pressure was raised and lowered over a standard range of 200 mm. between 530 and 730 mm. A group of 10 mosquitos was confined in a pressure chamber with a pressure of 730 mm. for five hours. A control count of

TABLE VI.

Comparison of the flight activity of mosquitos following various rates of rising and falling pressures.

		Increasing pressure					Decreasing pressure				
Experiment		(1)	(2)	(3)	(4)	(5)	(1)	(2)	(3)	(4)	(5)
No. of flights during control period (2 min.) prior to pressure change		0	0	2	1	0	0	1	1	0	0
Time to increase pressure by 200 mm. in minutes		15	12	5·6	3·5	3	31·2	8·5	5·5	3·5	3
Average rate of pressure change (mm./min.)		13·3	16·5	36	57	65	6·4	24	36	57	66
Accumulation of no. of flights by the minute after the pressure change	Min.										
	½	1	0	0	0	0	0	0	0	0	4
	1	2	0	0	0	1	1	1	0	0	6
	1½	3	1	2	1	2	1	1	0	0	6
	2	3	1	2	1	2	1	2	0	0	6
	3	4	1	3	1	2	1	2	2	1	7
	4	6	2	4	1	2	1	2	2	2	7
	5	7	7	4	1	2	1	2	2	4	7
	6	9	7	5	2	3	1	3	2	7	7
	7	10	9	6	2	3	1	3	2	7	8
	8	13	10	6	5	3	2	3	2	7	9
	9	15	12	8	5	3	2	3	2	7	10
	10	16	13	9	7	3	2	3	2	7	10
No. of flights/minute		1·6	1·3	·9	·7	·3	·2	·3	·2	·7	1·0

Acclimatisation period preceding each pressure operation = 5 hr. Range of each pressure change between 530 and 730 mm., and *vice versa* = 200 mm.

the number of " take-offs " during a two-minute period at the end of the five-hour period was recorded to indicate the normality of behaviour before beginning the experiment. The pressure was lowered to 530 mm. at a rate which was calculated by clocking the operation. Immediately following the completion of the drop in pressure the number of " take-offs " was recorded on a cumulative basis at 1-minute intervals during a 10-minute period. The same mosquitos were allowed to remain at the 530 mm. level for a five-hour period which was followed by a second two-minute control count of the " take-offs ". The pressure was raised to 730 mm. at a rate calculated by clocking the operation. Immediately following the completion of the rise in pressure the number of " take-offs " was recorded on a cumulative basis at 1-minute intervals during a 10-minute period.

Five experiments following this procedure were performed using a different group of mosquitos of approximately the same age for each experiment. The results for various rates of rising and falling pressures are tabulated in Table VI and plotted in fig. 8. For an increasing pressure the lower rates of change (less than 20 mm./min.) were the more effective in stimulating the mosquito to " take-off ". For decreasing pressure, the higher rates of change were found to be the more effective. It should be emphasised that the relations just mentioned were found for pressures below the mean atmospheric pressure recorded each month for the locality in which the experiments were conducted. Duplication of these experiments at pressure levels above the normal atmospheric level was found to be impossible with the manually-controlled pressure system used.

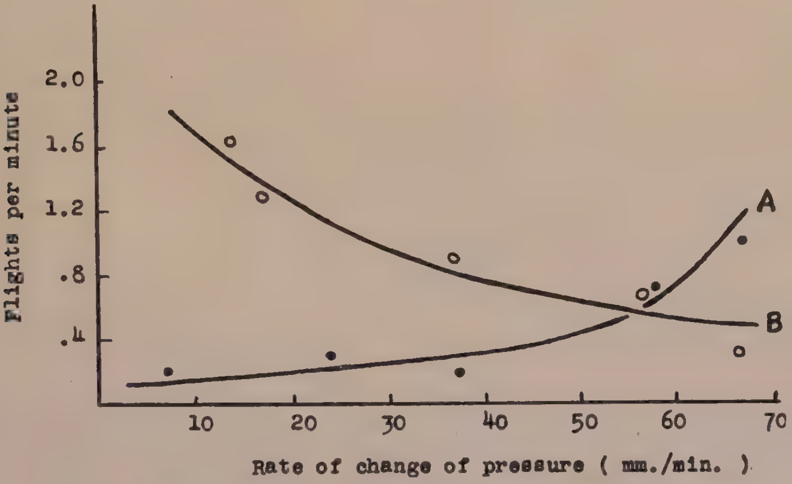


Fig. 8.—Graphs showing the number of flights/min. of 10 female mosquitos during a 10-minute period following the completion of a pressure change of 200 mm. at various rates. (A) Decreasing pressure. (B) Increasing pressure.

Effect of static pressures on flight activity.

On the basis of experiments on the acclimatisation of mosquitos to the various components of pressure, pressure level *per se* was found to have no effect on the flight activity of mosquitos unless associated with a rising or falling pressure. The values which determine the lowest curve in fig. 6 show that the flight activities after complete acclimatisation are not significantly different when they are compared at various pressure levels between 550 mm. and 800 mm. Experience showed in all experiments that flight activity depended on pressure level both during and up to three to six hours after a pressure change.

Discussion.

Although the effects of atmospheric pressure on the flight activity of *A. aegypti* are probably of less importance than those of temperature and saturation deficiency, they were found to be sufficiently significant in this investigation to be considered as an important factor. Though experience frequently indicated that the sensitivity to pressure varied with the temperature, attempts to correlate it with this and other meteorological factors were not included in these experiments.

Acclimatisation of the mosquito was found to be an important factor in the effect of pressure on flight activity. In these tests it was impossible to predict flight behaviour with accuracy unless sufficient time was allowed for completion of acclimatisation preceding each new pressure condition. An incompletely acclimatised mosquito exhibited random behaviour or even opposite behaviour for duplicate pressure conditions. It is possible that the irregular pattern of insect behaviour in the field under apparently similar pressure conditions may be due to incomplete acclimatisation of the insect to one natural barometric condition before exposure to a barometric change.

Provided the mosquitos were completely acclimatised before their exposure to any new pressure condition, the effect of a decreasing pressure was more stimulatory than that of an increasing pressure for pressures above 735 mm., while below 735 mm. the opposite relation obtained. There were indications in some experiments that this critical level may vary as an individual, physical characteristic rather than as a specific characteristic. This suggestion is supported by the experience that duplication of behaviour was often impossible unless mosquitos used in any one experiment were restricted to a short period of emergence during which atmospheric pressure was stable to within ± 1 mb. For this reason, experimental groups of mosquitos were selected from a population which emerged during a period of eight hours or less on days when atmospheric turbulence was minimum.

The reversal of the effects of pressure on flight activity shown by *A. aegypti* at 735 mm. may be significant in accounting for controversial literature on the effects of increasing and decreasing pressure on insect behaviour (Glick, 1939; Parman, 1920; Pictet, 1918; Williams, 1940; and others). Experiments with *A. aegypti* indicated that either decreasing or increasing pressure might be described in field studies as stimulating greater flight activity for this species, depending on the relation of the average pressure level obtaining at the time to the critical pressure level for the general population being studied. The large difference in variability of flight behaviour between individuals from a single brood and individuals from different broods emphasised the importance of the past history of a mosquito in the effect of pressure on its flight activity. There is some circumstantial evidence for the suggestion that the effect of atmospheric pressure on the flight activity of mosquitos may depend on physical characteristics of the individual acquired at the time of emergence. In the laboratory investigations with *A. aegypti*, the mean pressure level during the experiments was approximately 745 mm. during the months of December and January as compared with 735 mm. during February and March. The points represented in fig. 7 have been examined, and it was found that those obtained in December and January are situated to the left of the plotted line and indicate a critical pressure level of approximately 745 mm. Those obtained in February and March fall to the right of the line and indicate a lower critical pressure level. The regularity shown in this variation of behaviour suggests that the disposition of these points in relation to contrasting pressure conditions for the two periods may be significant.

It is significant also that the effects of a changing pressure on patterns of behaviour became negligible at 500–550 mm. At pressures below this level activity was random in nature; after a six-hour period of acclimatisation there was no difference between the effect of rising and the effect of falling pressure on the number of "take-offs". The results of experiments conducted at pressures between 500 mm. and 600 mm. were difficult to duplicate as compared to experiments conducted at higher levels. Below the 500 mm. level even instantaneous surges of pressure failed to stimulate flight provided the mosquito was acclimatised for at least six hours. Experiments indicated that completely acclimatised mosquitos were most easily and most consistently influenced by pressures that approximated atmospheric pressures in nature. Mosquitos became less consistent in their behaviour as their environmental air pressure departed from the mean pressure usually recorded in the laboratory.

Summary.

Laboratory investigations with the mosquito *Aëdes aegypti* (L.) have shown that air pressure has the following effects on flight activity:

The effects of pressure changes are consistently large enough to constitute an important factor in determining activity provided the mosquitos are acclimatised first to a particular pressure level.

The period of constant conditions necessary for complete acclimatisation was between three and six hours for all pressure conditions investigated.

When the period of acclimatisation had been fulfilled, the flight activity was approximately the same at all levels of static pressure investigated between 550 mm. and 800 mm. Hg.

After complete acclimatisation the activity following a moderate decrease in pressure was 1·5 to 2·4 times that following a similar increase in pressure when the general pressure level exceeded 735 mm. Hg.

When the general pressure level was less than 735 mm. Hg., the activity following a decrease in pressure was less than that following an increase; it would appear that 735 mm. is a critical pressure level for the stock of *A. aegypti* employed.

The activity during a uniform rise in pressure from 530 mm. to 730 mm. at 7·7 mm./min. was at least 10 times that during a reverse fall in pressure at the same uniform rate.

Provided the rate of change was not greater than 1 mm./sec., the maximum flight activity for falling pressures was observed at 780 mm. while the maximum for rising pressures was observed at 735 mm.

A pressure change of 15 mm. at approximately 1 mm./sec. was 2·5 times as stimulatory as one of 30 mm. at the same rate upon flight activity in the 30-minute period following the change.

At pressure levels between 530 mm. and 730 mm., the lower rates of increasing pressure were more stimulatory than the higher rates; but the higher rates of decreasing pressure were more stimulatory than the lower rates.

For mosquitos with a post-emergence age of four days, the variability of flight activity between individual mosquitos emerging on different days was three times that between individuals emerging the same day from the same brood.

Acknowledgements.

The author is indebted to Dr. A. W. A. Brown, Head, Department of Zoology, University of Western Ontario, for his helpful advice and criticism throughout the investigation of the problem and the preparation of the paper. Appreciation is gratefully extended to F. Jursic, Department of Zoology, University of Western Ontario, for his assistance in maintaining the material necessary for the experiments, and to my wife, for her faithful assistance in the tedious task of making

the lengthy observations of behaviour and recording the results. Thanks are extended to Dr. Hubert Martin, and Dr. B. N. Smallman, Science Service Laboratory, London, for their courtesy in providing accommodation for some of the experiments herein described.

References.

Back, E. A. & Cotton, R. T. (1925). The use of vacuum for insect control.—J. agric. Res., **31,** pp. 1035–1041.

Cleveland, L. R. (1925). Toxicity of oxygen for Protozoa in vivo and in vitro; animals defaunated without injury.—Biol. Bull., Wood's Hole, **48,** pp. 455–468.

Cole, F. J. (1906). The bionomics of grain weevils.—J. econ. Biol., **1,** pp. 63–71.

Glick, P. A. (1939). The distribution of insects, spiders and mites in the air.—Tech. Bull. U.S. Dep. Agric., no. 673, 150 pp.

Greenwood, M. jr. (1906). The effects of rapid decompression on larvae.—J. Physiol., **35,** (vi).

Herrera, A. L. & Lope, D. V. (1899). La vie sur les hauts plateaux.—Mexico City.

Huber, F. (1814). Nouvelles observations sur les abeilles.—2nd edn., 2 vols. Paris.

Lehmann, N. & Vaney, C. (1911). Relations entre les conditions climatériques et la fréquence des larves de l'hypoderme du boeuf.—C. R. Acad. Sci., Paris, **152,** pp. 1508–1510.

Lutz, F. E. (1929). Experiments with " wonder creatures ".—Nat. Hist., N.Y., **29,** pp. 160–168.

Parman, D. C. (1920). Observations on the effect of storm phenomena on insect activity.—J. econ. Ent., **13,** pp. 339–343.

Pictet, A. (1918). Le développement des Lépidoptères : le rôle de la température en relation avec la pression barométrique.—C. R. Soc. Phys. Hist. nat. Genève, **34,** pp. 32–34.

Roller, L. W. (1906). Respiratory responses in the grasshopper to variations in pressure.—Kans. Univ. Sci. Bull., **3,** pp. 211–221.

Wellington, W. G. (1944). Barotaxis in Diptera, and its possible significance to economic entomology.—Nature, Lond., **154,** pp. 671–672.

Wellington, W. G. (1945). Conditions governing the distribution of insects in the free atmosphere. Pt. I. Atmospheric pressure, temperature and humidity.—Canad. Ent., **77,** pp. 7–15.

Wellington, W. G. (1946*a*). The effects of variations in atmospheric pressure upon insects.—Canad. J. Res., (D) **24,** pp. 51–70.

Wellington, W. G. (1946*b*). Some reactions of muscoid Diptera to changes in atmospheric pressure.—Canad. J. Res., (D) **24,** pp. 105–117.

Williams, C. B. (1940). An analysis of four years' captures of insects in a light trap. Pt. II. The effect of weather conditions on insect activity.—Trans. R. ent. Soc. Lond., **90,** pp. 227–306.

Woodworth, C. E. (1932). Some effects of reduced atmospheric pressure upon honey bee respiration.—J. econ. Ent., **25,** pp. 1036–1042.

Woodworth, C. E. (1936). Effect of reduced temperature and pressure on honey bee respiration.—J. econ. Ent., **29,** pp. 1128–1132.

HOST FINDING AND SELECTION BY *SPALANGIA DROSOPHILAE* ASHM.

By F. J. Simmonds.
Commonwealth Institute of Biological Control.

The biology of *Spalangia drosophilae* Ashm. has been described in previous papers (Simmonds, 1952, 1953*a*, *b*). In this paper the results will be given of experiments designed to determine the criteria by which an ovipositing female *Spalangia* (a) is attracted to and prevented from wandering away from an environment where hosts suitable for her progeny may be found, and (b) selects these hosts from among the various objects encountered. Among a number of previous investigations of these problems one might cite the works of Laing (1937, 1938), using *Trichogramma evanescens* Westw., a parasite of *Sitotroga cerealella* (Ol.) etc., Thorpe & Jones (1937) and Thorpe (1938) where the olfactory responses of various insects to a number of substances have been investigated, and Salt (1935, 1937, 1938) who dealt with the host relationships of *T. evanescens*.

The problem of superparasitism is a specialised aspect of host selection and has been investigated in *Spalangia* in some detail. This will be described elsewhere.

The behaviour of the parasite female prior to oviposition will be divided into two phases, namely host finding and host selection.

Host Finding.

In this section some of the factors involved in maintaining an ovipositing female *Spalangia* in an area where hosts are likely to be available will be discussed. The situation is somewhat different from that described by Laing for *Trichogramma* since no directive movements after the location of one host are likely to lead immediately to the finding of a second host. The problem seemed to be one of determining factors involved in attracting *Spalangia* adults to the bases of wheat plants and in preventing them from wandering far away from this environment. Following this there is the location of host puparia in this environment.

At first an attempt was made to " hide " hosts, to investigate the possibility of the degree of superparasitism varying when extensive periods of search occurred between the finding of successive host puparia. In order to simulate natural conditions to a certain extent, sections of waxed-paper " straws " 1 inch long were cut. Fresh *Drosophila* puparia (washed to remove odour partially) were placed singly halfway down the inside of ten such straw sections. These ten pieces were placed at random with 90 other similar empty sections in a half-pint milk bottle with the opening plugged with cotton-wool. Two mated female *Spalangia* were introduced into each bottle prepared in this way and left for 24 hours. At the end of this time the puparia were examined and dissected, the number of parasite eggs occurring in each being recorded. The results however, were not different from those obtained when ten hosts were exposed on squared paper to two *Spalangia* females for 24 hours. Thus with the set-up of these experiments the results of egg distribution were not complicated by any search factor. With an active insect like *Spalangia* laying only a few eggs a day, and capable of very marked restraint as has been shown with experiments to investigate superparasitism, such experiments would have to be designed so that the ovipositing female was able to find only one or two hosts per day. This would be an extreme condition to investigate, and might deviate considerably from anything found under natural conditions. Moreover, the results obtained on restraint indicate how such a search factor would act, at the point when it did occur.

In order to investigate the reactions of the female which might result in directing her to a location where suitable hosts are likely to occur, a number of individuals were placed in a " sensory gradient ". Several factors are brought immediately to mind which might be associated with, and possibly sensed by the female as directing influences towards such suitable environments—soil, dampness, wheat-plants, grass, etc. To investigate these possibilities two tubes were prepared of ½ inch glass tubing. The first (A) was 24 inches long; in the centre of this a hole was blown and at each end vials were fitted by means of pieces of very clean rubber tubing, the ends of the tube being separated from the vials by pieces of bolting silk. This tube was used for testing differential preferences between two materials. The second (B) was a simple glass tube ½ inch × 20 inches with a similar vial and rubber tubing arrangement at one end and a simple plug of cotton-wool at the other. Behind each tube was fixed a piece of wood, marked at 2-inch intervals so that the position of insects in the tubes could be recorded. This simple apparatus was placed in a dark room at 60°F. The darkness obviated complicating phototropic reactions caused by differential illumination, and the low temperature decreased the activity of the insects. Examinations were made in the dark by means of a small portable lamp, and between experiments the apparatus was thoroughly cleaned with hot water and alcohol and dried by sucking dry air through it. Each experiment was duplicated, using reverse ends of the tube for the attractants, so that any variation due to the glass tube itself would be counteracted. Numbers of *Spalangia* were introduced into the tube for each experiment and the substance or substances to be tested placed in the vials at the end. At intervals the tube was examined and

TABLE I.

* Details of observations of female *Spalangia* in tube with an attractant at one end. (Tube B.)

Time of observation	Time in hours	Number of *Spalangia* occurring in each 2″ graduation of the tube												Total
		Blank end						Attractant end						
		Total	5	4	3	2	1	1	2	3	4	5	Total	
4.30 p.m. 16th Feb.	3	11	7	—	1	1	2	3	—	—	1	13	17	28
9.30 a.m. 17th Feb.	17	8	5	2	—	—	1	1	1	2	3	20	27	35
Ends changed														
4.30 p.m. 17th Feb.	3	10	2	4	1	3	—	1	—	1	1	15	18	28
1.30 p.m. 18th Feb.	21	5	3	—	2	—	—	1	1	1	3	20	26	31
Total			17	6	4	4	3	6	2	4	8	68		122

* Attractant was *Drosophila* medium containing *Drosophila* larvae.

TABLE II.

Results of observations of *Spalangia* adults in glass tubes with different attractant materials at one end.

Tube "A"

Spalangia used	Attractant at one end	Number of *Spalangia* occurring in each 2″ graduation of the tube														Attractant at other end
		Total													Total	
Unmated females	Male *Spalangia*	10	1	2	1	5	1	—	2	3	1	2	2	14	24	Blank
Unmated males	Female *Spalangia*	33	21	1	3	1	3	4	1	1	1	—	3	15	21	Blank
Unmated males	Dry *Musca* puparia	31	17	5	3	5	1	—	1	—	—	2	12	31	46	Blank
Unmated females	Dry *Musca* puparia	14	9	3	—	1	—	1	—	—	1	1	4	25	31	Blank
Mated females	Dry *Drosophila* puparia on original paper	191	153	10	9	10	8	1	3	9	3	3	8	15	41	Blank
Mated males	Wheat leaves	122	37	22	18	13	20	12	6	2	5	1	16	26	56	Blank
Mated females	Sandy loam and humus ("Dry"—air at 75° F.)	157	130	8	7	9	2	1	—	—	2	1	2	1	6	Blank
Mated females	Sandy loam ("Dry"—air at 75° F.)	34	6	7	8	4	5	4	3	13	7	1	6	48	78	Water

TABLE II (continued).

Tube " *B* "

Spalangia used	Attractant at one end	Number of *Spalangia* occurring in each 2″ graduation of the tube											
		Total	Attractant end					Blank					Total
Mated females	*Drosophila* medium and larvae	88	68	8	4	2	6	3	4	4	6	17	34
Unmated females	Water	141	126	5	7	1	2	2	4	4	6	10	26
Mated females	Dry, empty, parasitised *Drosophila* puparia	67	35	6	3	5	18	7	2	2	4	34	49

the position of the insects with respect to the graduations on the wooden backing to the tube recorded.

To illustrate the use of this apparatus the experiment in which *Drosophila* medium containing *Drosophila* larvae was tested against " blank " will be given in detail. Tube B was used, the small shell vial being half filled with *Drosophila* medium containing larvae. Thirty-five day-old mated females of *Spalangia* which had had no previous contacts with hosts were introduced into the tube at 1.30 p.m. and their positions noted at 4.30 p.m. and at 9.30 a.m. the following day. At this point the apparatus was cleaned and the medium placed at the reverse end of the tube. The results are given below (Table I). It is noticeable that the same total number of *Spalangia* is not recorded at each observation. This is due to the necessity for an observation of short duration with a small lamp, so that the insects will not be disturbed.

It is obvious that in this experiment the changing of ends makes little or no difference to the final result, and hence the two pairs have not been considered separately. It is obvious too that *Drosophila* medium exerts a strong attraction for the females. It is seen that at the " blank " end a number of females congregate on the cloth,—obviously once they gain a foothold on the rough surface of the cloth they are loth to relinquish it for the smooth glass walls of the tube. This constitutes a slight complicating factor, but the increase in number at the attractant end in the second period of 17 hours shows that movement still occurs in spite of this.

A consideration of Table II enables a number of conclusions to be drawn as to environments which are liable to attract *Spalangia*. Dampness, *Drosophila* larvae in their medium, *Drosophila* puparia covered with the remnants of dried medium, and a dried mixture of sandy loam and humus are all attractive to female *Spalangia*, and when water and the sandy loam mixture are offered, water proves more attractive. Wheat leaves are attractive to mated females. Dry empty parasitised *Drosophila* puparia are neither attractive nor repellent; dry living *Musca* puparia are mildly repellent both to male and female *Spalangia*, unmated males are not specially attracted to the presence of the females and the females are apparently repelled by that of the males.

Where water was used as an attractant the females did not congregate at the extreme end of the tube but about half an inch from it. This indicates a fine sensitivity to humidity, enabling them to select a very damp environment but avoiding 100 per cent. humidity. In general, the females are attracted to the soil, preferably where there is high humidity. In the field this would draw them to the base of vegetation which would consist for the most part of grasses where suitable host puparia are likely to be found. Thus the problem of how the individuals *congregate* in an area most suitable to the finding of host material resolves itself into the study of the preferenda of the species with regard to several fairly well defined factors such as humidity and presence of soil. Possibly following these general preferenda there are further factors such as phototropism and thigmotropism which would bring the parasites into micro-environments where the finding of hosts is still more likely.

Once in this general type of location where hosts might be expected to occur it would appear from observation that the finding of a host puparium is largely by chance. In areas where hosts actually occur, a female parasite wanders around apparently aimlessly until very close (3–4 millimetres) to a host puparium when some excitement is shown and directive movements towards the host are made. After a possible host has been found there follows an examination of it by the female to determine if in fact it is suitable for her progeny.

Host Selection.

In order to gain some idea of the general characters that must be possessed by a host if it is to be successfully attacked by *Spalangia*, and in order to determine in some measure the likelihood of the species becoming secondarily parasitic, a number of different hosts were offered to ovipositing females. Several such females were placed in the usual type of oviposition vials with a number of the following:— Puparia of *Musca domestica* L., *Zenillia caesar* (Ald.), and a large unidentified Drosophilid; pupae of *Loxostege sticticalis* (L.), *Cydia pomonella* (L.), *Pyrausta nubilalis* (Hb.), and *Ephestia kuehniella* Zell.; cocoons of *Ephialtes caudatus* (Ratz.), *Cryptus sexannulatus* Grav., *Phytodietus pulcherrimus* (Cress.) and *Triaspis thoracicus* (Curt.). The females attempted to sting the Lepidopterous pupae, and sometimes apparently succeeded in piercing the chitin with the ovipositor. The pupae were not paralysed, however, and no eggs were laid. In the case of *Musca* and *Zenillia*, attacks were more frequent, stinging occurred, and some eggs were laid. A single adult was reared from a *Musca* puparium, but, in general, development of the fly was not arrested when the pupa was stung by the parasite, and neither of these two species is suitable as a host. The large Drosophilid was readily attacked and it proved a suitable host. None of the Hymenopterous cocoons was attacked. The rearing experiments in the summer of 1942 indicated that in the field *Spalangia* develops only extremely rarely at the expense of *Hexacola* and *Loxotropa*, two other parasites of *Oscinella frit* (L.). The facts presented above indicate that, as far as was tested, the number of different hosts attacked by *Spalangia* is comparatively limited. Apart from the species mentioned above as hosts there are, of course, *Oscinella* and *Drosophila* puparia. No preference tests between these last two have been made.

Thus the general type of suitable host consists of a small pupa enclosed in an outer chitinous wall, with a space between the two. *Spalangia* will attack hosts which are apparently suitable except that they are too large (*e.g.*, *Musca*) and are partially interested in Lepidopterous pupae, though only initial examination occurs, the pupae then being rejected as unsuitable. It will be shown below that even when these " primary " criteria are satisfied a host may be rejected if the pupa within the outer wall is not living, as in the case of already parasitised, stung, or " coddled " *Drosophila* puparia. Though the female generally oviposits only on hosts suitable for the completion of development of her progeny, there appear to be certain characters which cause the females to exhibit some degree of interest in different hosts, which finally prove to be unsuitable. Thus it would seem that the females examine anything that even vaguely resembles a suitable host, *e.g.*, Lepidopterous pupae, large Dipterous puparia, etc., and eliminate them

TABLE III.

Results from exposing *Drosophila* puparia of different ages to ovipositing female *Spalangia*.

Hosts exposed to ovipositing female *Spalangia*	Younger puparia				Older puparia			
Comparison between hosts of two ages in hours (no. in brackets)	Unattacked	Stung	Parasitised	Dead	Unattacked	Stung	Parasitised	Dead
0–24 (200) and 24–48 (200) ..	104	5	79	12	86	11	88	15
0–24 (176) and 48–72 (174) ..	85	4	87	—	72	9	91	2
24–48 (225) and 48–72 (225) ..	101	9	110	5	67	15	141	2

only after an examination varying in duration and intensity with the suitability of the host. There is no "all or nothing" acceptance or rejection of possible hosts, but a graded response varying with host suitability.

Whether the female reacts to the host as a whole or to certain definite characters is uncertain. However, in the final discrimination between healthy and parasitised, stung, or coddled hosts described below it would seem as though single definite characters were being sensed.

After obtaining these general results as to the type of host required by *Spalangia*, further experiments were set up to investigate the preferences for different ages of puparia of *Drosophila*. At 75°F. *Drosophila* remains in the puparium for about 4·5 days (50 per cent. emergence) and, for the tests, puparia were removed from stock cultures so as to be 0–24, 24–48, and 48–72 hours old. These were stuck with water onto squared paper in 25's, 12 of one age and 13 of another, alternating as in the fig. 1.

· X · X ·
X · X · X
· X · X ·
X · X · X
· X · X ·
X · X · X
· X · X ·
X · X · X
· X · X ·
X · X · X

Fig. 1.—Position of two types of host puparia in host-selection experiments.

These squares of paper were placed in oviposition vials (Simmonds, 1952). Two ovipositing female *Spalangia* were introduced into each and left for 24 hours. The numbers of puparia of each age which had been attacked were then noted. It must be pointed out that, owing to the fact that parasites were left with the puparia for 24 hours, these aged during the experiments and this detracts from the value of the results. It was thought that, if any positive result were obtained, further experiments could investigate this point more fully. The results obtained are given in Table III.

It is seen that all healthy puparia of *Drosophila* containing pupae appear acceptable, and that differences in age of puparia within the limits tried have little or no influence on their acceptability. It was found that very fresh puparia containing unchanged larvae were rejected as hosts when older puparia were present, although they were attacked if more suitable hosts were not available. They were stung and paralysed, and in some cases eggs were laid within the larva; these eggs, however, did not develop. In the case of these early puparia one of the "primary" conditions of host suitability is not fulfilled, namely, there is no space between the puparial wall and the actual host.

In an endeavour to decide more exactly the criteria by which a generally suitable host was accepted or rejected by an ovipositing female, particularly in connection with the sensory impressions involved in the avoidance of superparasitism, further experiments were carried out giving ovipositing females a choice between various types of possible hosts. Two types of host were alternated on squared paper, equidistant $\frac{1}{4}$ inch from each other, and exposed to two ovipositing *Spalangia* females in a $4\frac{1}{2} \times 1$ inch vial, the cork of which had damp cotton-wool and a raisin on it. After 24 hours the hosts were removed and examined. Four choices were offered, details of which follow.

1. *Alternating unparasitised and fresh singly-parasitised puparia.*

The results are given in Table IV. In the last three individual experiments where high parasitism occurred, restraint broke down and under these circumstances it appears that very freshly parasitised puparia are preferable to those parasitised some time previously, since superparasitism occurred ten times in the more newly parasitised group, as compared with only once, and that only in an experiment where all fresh hosts had been parasitised, in the group which by the end of the experiment had been parasitised for 24 hours. It is quite obvious that the ovipositing female *Spalangia* can distinguish between parasitised and healthy hosts, and can avoid ovipositing in the former when both types are present.

TABLE IV.

* Results from exposing alternating unparasitised and fresh singly-parasitised hosts to ovipositing female *Spalangia*.

Numbers puparia presented		Results							
		Unparasitised					Parasitised		
Unparasitised	Parasitised	U.	St.	P.	D.	Eggs laid	Unchanged	Superparasitised	Eggs laid
7	7	2	1	4	—	4	7	—	—
12	13	6	4	1	1	1	13	—	—
13	12	3	2	7	1	7	12	—	—
12	13	—	—	10	2	16	13	—	—
13	12	1	1	11	—	12	12	—	—
12	12	—	1	11	—	14	12	1	1
69	69	12	9	44	4	54	69	1	1

* In this and succeeding Tables, U. indicates puparia that are unchanged, St. those that are "stung only", P. those that have been actually parasitised, and D. those that have died.

2. *Alternating unparasitised puparia and those that are stung only.*

Experiments were set up as before, but with alternated unparasitised puparia and those that had been "stung only" 24 hours previously (Table V). There is a very definite avoidance of oviposition in hosts that are "stung only" when healthy hosts are also present.

TABLE V.

Results from exposing alternating unparasitised hosts and those that have been "stung only".

Unparasitised puparia						Stung puparia					
Number	U.	St.	P.	D.	Eggs laid	Number	U.	St.	P.	D.	Eggs laid
13	1	2	10	—	12	12	—	11	1	—	1
12	3	2	6	1	6	13	—	13	—	—	—
25	4	4	16	1	18	25	—	24	1	—	1

3. *Alternating fresh singly-parasitised puparia and fresh "stung only".*

From the above results there arises the question as to whether parasitised puparia are less acceptable as hosts than those that are "stung only".

Experiments were set up as before but alternating fresh parasitised and fresh "stung only" puparia. Results are shown in Table VI.

TABLE VI.

Results from exposing alternating "stung only" and parasitised hosts to ovipositing female *Spalangia*.

Stung puparia				Parasitised puparia			
Number	Unchanged	Parasitised	Eggs laid	Number	Unchanged	Superparasitised	Eggs laid
13	11	2	3	12	6	6	8
13	12	1	2	12	11	1	3
12	10	2	2	13	12	1	1

The "stung only" puparia are not more acceptable as hosts than parasitised puparia to ovipositing female *Spalangia*. Hence the point during an oviposition attack at which "immunity" from superparasitism is conferred is that at which the host is stung and not when an egg is laid. The senses of the ovipositing female parasite may react to the host as a whole and recognise it as "stung", or the rejection of such a host may be due to one or more definite stimuli, *e.g.*, (1) Smell on the outside of the puparium of host body fluid clotted around the puncture of the previous stabbing. (2) Smell of fluid left by the ovipositor, *i.e.*, fluid originating from the female *Spalangia*. (3) On thrusting the ovipositor into the host the immobility, or some change in chemical composition of the body fluids of the paralysed host may be detected. (4) A number of such stimuli may form a pattern causing rejection.

This was further investigated by alternating experiments. A number of *Drosophila* puparia were coddled by placing them in water at 120°F. for one minute, when they were killed and had the appearance of paralysed hosts, decomposition being long delayed.

4. *Alternating healthy and coddled puparia.*

Coddled puparia were alternated with healthy hosts on papers, and exposed to female *Spalangia* as before. The results are shown in Table VII.

TABLE VII.

Results from exposing alternating coddled and healthy hosts to ovipositing female *Spalangia*.

Healthy puparia						Coddled puparia					
Number	U.	St.	P.	D.	Eggs laid	Number	U.	St.	P.	D.	Eggs laid
13	—	1	12	—	14	12	9	1	2	—	2
13	—	—	13	—	15	12	9	—	3	—	3
26		1	25		29	24	18	1	5		5

Coddled puparia are unacceptable to ovipositing *Spalangia* when offered with fresh living puparia. In this case there has been no contact between the coddled hosts and *Spalangia* that could account for their unacceptability. The coddled puparia are quite suitable for development of *Spalangia*, and the ovipositing female parasite is avoiding a suitable host. This is indicative of a choice being made by the female on the grounds of some fairly restricted difference between a healthy and a coddled puparium, and is in contrast to the condition found by Lloyd (1938) in the case of *Ooencyrtus* parasitising eggs of *Lymantria dispar* (L.) where coddled eggs were readily accepted, and " the disparity between the oviposition in these two types is not sufficient to justify the conclusion that dead hosts will usually be avoided in the field ".

It may be argued that the factors causing avoidance of a coddled host are different from those causing rejection of a " stung host ", but this seems unlikely. If the complex of factors is the same it is apparent that enough similarity exists between coddled and stung puparia to render both unacceptable to ovipositing *Spalangia*. The *apparent* difference between the two types is that of the actual traces of attack by the *Spalangia* in the case of stung puparia. This would indicate that odour left by the female, of exudate from punctured host or from ovipositor, is not of primary importance in rendering the puparia unacceptable to *Spalangia*. The obvious similarity between them is the death of the pupa. It is unlikely that the chemical changes occurring after coddling and stinging are identical, and the most obvious difference between the living puparia and both coddled and stung ones is the cessation of heart-beat. It is important to notice that, as far as can be judged, the coddled puparia were rejected on purely antennal examination before the ovipositor was inserted into the host but, although the punctures formed by stinging are sometimes visible, it is not certain that they can always be seen. Subject, however, to this, it therefore seems probable that the discerning sense is located in the antennae, somewhere where it is effective external to the puparium.

Summary.

Experiments were designed to determine the criteria by which an ovipositing female of *Spalangia drosophilae* Ashm. is attracted to an environment where suitable hosts may be found, and by which these hosts are selected.

The results obtained indicate that ovipositing female *Spalangia* are attracted to and maintained in areas where suitable host puparia may occur by their reaction to sensory impressions. Thus females tend to be attracted to dampness and to soil level where, in grasses, host material is likely to be found. In such an area searching for hosts appears to be at random, but once an object that is a possible host is located there follows a careful examination and, if the object is " considered " a suitable host, oviposition follows. It appears that there are several definite criteria by which an object is accepted as a host suitable for oviposition. In general the hosts selected by the parasite are only those which are suitable for the development of her progeny.

References.

Laing, J. (1937). Host-finding by insect parasites. 1. Observations on the finding of hosts by *Alysia manducator*, *Mormoniella vitripennis* and *Trichogramma evanescens*.—J. Anim. Ecol., **6**, pp. 298–317.

Laing, J. (1938). Host-finding by insect parasites. 2. The chance of *Trichogramma evanescens* finding its hosts.—J. exp. Biol., **15**, pp. 281–302.

Lloyd, D. C. (1938). A study of some factors governing the choice of hosts and distribution of progeny by the Chalcid *Ooencyrtus kuvanae* Howard.—Phil. Trans., (B) **229,** pp. 275–322.

Salt, G. (1935). Experimental studies in insect parasitism. III. Host selection. —Proc. roy. Soc., (B) **117,** pp. 413–435.

Salt, G. (1937). Experimental studies in insect parasitism. V. The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts.—Proc. roy. Soc., (B) **122,** pp. 57–75.

Salt, G. (1938). Experimental studies in insect parasitism. VI. Host suitability. —Bull. ent. Res., **29,** pp. 223–246.

Simmonds, F. J. (1952). Parasites of the frit-fly, *Oscinella frit* (L.), in eastern North America.—Bull. ent. Res., **43,** pp. 503–542.

Simmonds, F. J. (1953*a*). Inter-relationships of the parasites of the frit-fly, *Oscinella frit* (L.), in eastern North America.—Bull. ent. Res., **44,** pp. 387–393.

Simmonds, F. J. (1953*b*). Observations on the biology and mass-breeding of *Spalangia drosophilae* Ashm. (Hymenoptera, Spalangiidae), a parasite of the frit-fly, *Oscinella frit* (L.).—Bull. ent. Res., **44,** pp. 773–778.

Thorpe, W. H. (1938). Further experiments on olfactory conditioning in a parasitic insect. The nature of the conditioning process.—Proc. roy. Soc., (B) **126,** pp. 370–397.

Thorpe, W. H. & Jones, F. G. W. (1937). Olfactory conditioning in a parasitic insect and its relation to the problem of host selection.—Proc. roy. Soc., (B) **124,** pp. 56–81.

QUANTITIES OF FOOD EATEN BY THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSK.), IN RELATION TO GROWTH.

By P. M. Davey, M.Sc.*

E.M.I.

Anti-Locust Research Centre.

In the field, hoppers of the Desert Locust, *Schistocerca gregaria* (Forsk.), feed principally on low-growing annual herbs with a relatively high water-content, rather than on grasses (Brown, 1947). Lists of plants eaten by it have been published by Husain, Mathur & Roonwal (1949) who have also investigated the quantities of fig leaf eaten. However, grass has proved to be adequate for laboratory breeding of this species, and knowledge of the quantity of grass necessary for a locust to reach a given stage in its life-history is of importance to laboratory workers. The principal aim of the present work has been to obtain a complete assessment of the quantity of fresh grass eaten by *S. gregaria* from hatching to maturity of the adults under laboratory conditions.

Since dry bran baits are widely used in anti-locust campaigns (Gunn, 1952), the weights of wheat bran eaten during a specified time by hoppers of certain instars have been ascertained and are given here, together with the weights and body-lengths of all the hopper instars.

The Weight of Fresh Grass Eaten.

Materials and techniques.

The locusts used in the experiments were the progeny of some obtained from British Somaliland in 1946 and Cairo in 1949. The eggs, laid by crowded adults, were incubated at 34·5°C. and the hoppers were reared in cylindrical celluloid cages 38 cm. high and 20 cm. in diameter (*i.e.*, with a capacity of about 12 litres), the lids of which were made of zinc gauze (30 mesh per inch). The food supplied to the hoppers was fresh grass, mainly *Poa* sp., *Phleum pratense* and *Agropyron repens*, obtained from a sewage farm. The grass was kept fresh for the young hoppers by standing the ends of the blades in water, but this was not necessary for the routine rearing of the older hoppers and adults.

Hoppers to be used in an experiment were observed hatching over a period of two hours; their sex was determined (without anaesthetisation) and they were weighed in groups on an aperiodic balance reading to 0·2 mg.

In the first experiment (Experiment I), six groups of 12 males each and six of 12 females each were set up in the large celluloid cylinders already described. The number of hoppers per group was as large as possible to allow for individual variation; groups of 12 are easy to handle and eat appreciable quantities of food. During the experiment, mortality of the hoppers occurred, but the number per cylinder was maintained above eight by amalgamation of the hoppers from two or more cylinders. Also, newly fledged deformed adults were discarded and this left approximately two-thirds of the original number of locusts; very few of these died before reaching maturity.

The cylinders were arranged in groups and those of each group were placed round a 150-watt electric light bulb so that the centre line of each cage was about

---

*Now at the Pest Infestation Laboratory of the Department of Scientific and Industrial Research.

17 cm. from the centre line of the bulb. Temperature and relative-humidity readings were taken, before the bulbs were switched on in the morning and before they were switched off seven hours later, by means of a mercury-bulb thermometer and an Edney paper hygrometer, suspended in the centre line of one of the cages in each group. The temperature of the room was thermostatically controlled; the average night-time temperature was 28·5°C. and the average day-time temperature was 39·5°C. The weighted mean temperature over the 24-hour period was thus 31·7°C. The weighted mean relative humidity calculated in the same way was 50 per cent.

Grass for the groups of hoppers in the cylinders was weighed, to 0·1 mg., in a screw-cap aluminium weighing bottle, on each day from hatching to maturity of the adults. Care was taken to select blades of grass that were fresh and uniformly green. The stalks were discarded because they have a higher water content than the blades and are less readily eaten by the hoppers. The grass was always washed in tap water and superficially dried with blotting paper before being weighed. The ends of the weighed grass were inserted into a container of water to reduce desiccation.

In order to ensure that the weighed grass was made available to the hoppers for the same length of time each day, the grass remaining uneaten was removed from the cages as soon as the light bulbs were switched on in the morning, and the ration for the next 24 hours was placed in the cages two hours later. From preliminary experiments, it was deduced that this enforced abstinence would not introduce a starvation factor since the natural pauses between feeds of first-instar hoppers can last up to 274 minutes. The hoppers of each cage were weighed about four hours after the daily ration had been placed in the cage. The older hoppers ate most of the grass that was not submerged, but hoppers in the first, second and third instars ate only some of it; since errors due to desiccation were great, the results for these instars were discarded and special techniques were

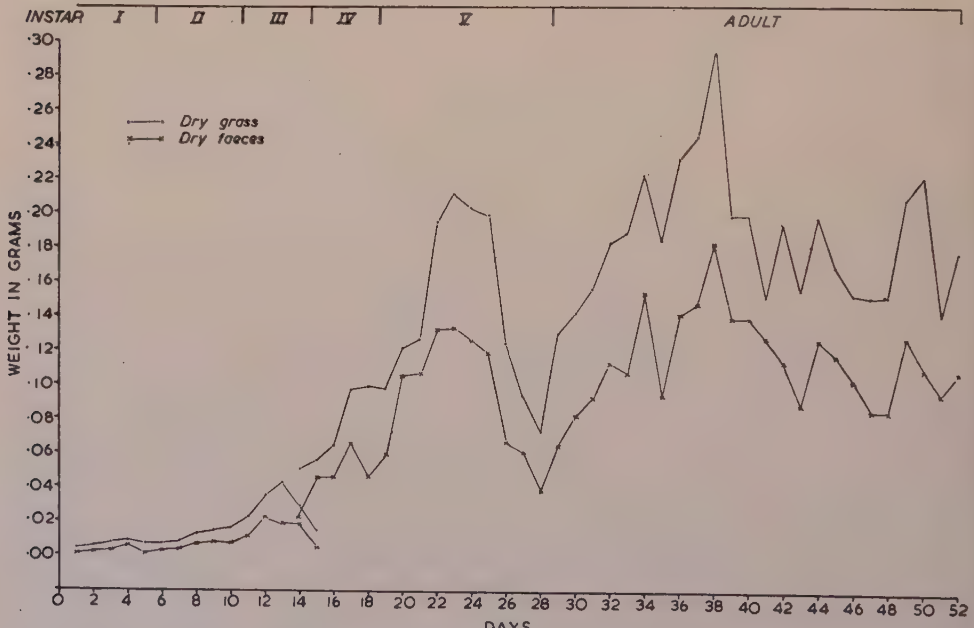


Fig. 1.—Dry weight of grass eaten and faeces expelled by developing *Schistocerca gregaria* Forsk.

devised for obtaining more accurate information about the quantities eaten by the young hoppers and were used in a second experiment (Experiment II).

In Experiment II each replicate consisted of three hoppers. In the first and second instars the sexes were not separated, although they were afterwards found to be present in approximately equal numbers, and the hoppers were set up in a glass tube 8 cm. high and 2¼ cm. in diameter. In the third instar the sexes were separated and confined, again in groups of three, in celluloid cylinders of the same proportions as the glass tubes but eight times their capacity, the volume of the third-instar hopper being approximately eight times that of the first. Caps of zinc gauze (8 mesh per inch) were made for these cylinders. Six of the glass tubes or three of the celluloid cylinders of each series were symmetrically arranged inside a large celluloid cylinder so that they were equidistant from a 150-watt bulb. The hoppers were weighed daily before being offered small weighed quantities of grass (0·1–1·0 gm.); the ends of the blades were stood in phials of water.

Throughout all experiments the uneaten grass removed daily was again washed in tap water, superficially dried with blotting paper and immediately weighed. When the hoppers were removed for weighing, the faeces were collected, dried for 24 hours at 95°C. and weighed, and the dry weight of the residual grass from each cage and the two control samples was similarly determined. The percentage dry-to-wet weight of residual grass was used to estimate the dry weight of grass eaten; the mean percentage dry matter of the residual grass was 16·3 and of the controls 16·1.

The results are given in fig. 1, and show the close correspondence between the estimated dry weight of grass eaten and faeces expelled.

The quantities of grass eaten by hoppers and adults.

In calculating the results, the observations on all the cages were averaged for each day, since there was found to be no significant heterogeneity at the 5 per cent. level between the six groups of hoppers used in Experiment I as regards the weights of grass eaten, expressed in gm. per gm. body weight, on day 14 to day 29 inclusive. The results are shown in fig. 2.

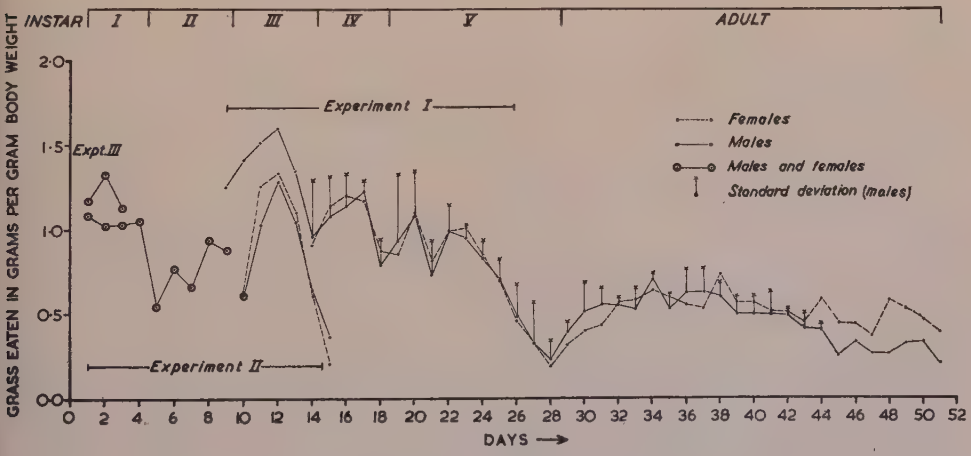


Fig. 2.—Average weight (gm. per gm. body weight) of fresh grass eaten by males and females of *Schistocerca gregaria* Forsk.

The hoppers did not all moult on the same day and there was considerable overlapping of consecutive instars both within and between cages; more of the hoppers of the earlier instars moulted concurrently than of the later ones, in which there was a lag of three or four days. The overlapping of instars tends to smooth out the feeding curve; nevertheless, fig. 2 shows marked reductions in the quantities eaten on the day before that on which most of the hoppers moulted and vigorous resumption of feeding after moulting, thus agreeing with the results of Ellis (1951) for *Locusta migratoria migratorioides* (R. & F.). In fig. 2 there is a false peak at the beginning of the fifth instar, due to the inadvertent supply of extra heat on day 20.

Although the male and female hoppers eat similar quantities of grass per unit body weight, the growth rate of the females is greater than that of the males (p. 545), and the absolute weight of grass eaten by females is greater than that eaten by males, from at least the third instar (fig. 3). From the 44th day after hatching, when the pink colour of the young adults was disappearing and the males had atttained their maximum weight (fig. 7), they ate significantly less per unit of body weight than the females. The average total weights of fresh grass eaten by hoppers between hatching and becoming adult have been calculated as 10·2 gm. for males and 12·9 gm. for females, and by adults between moulting and maturing as 20·5 gm. for males and 31·4 gm. for females. The total consumption between hatching and becoming mature thus averages about 30·7 gm. for males and 44·3 gm. for females.

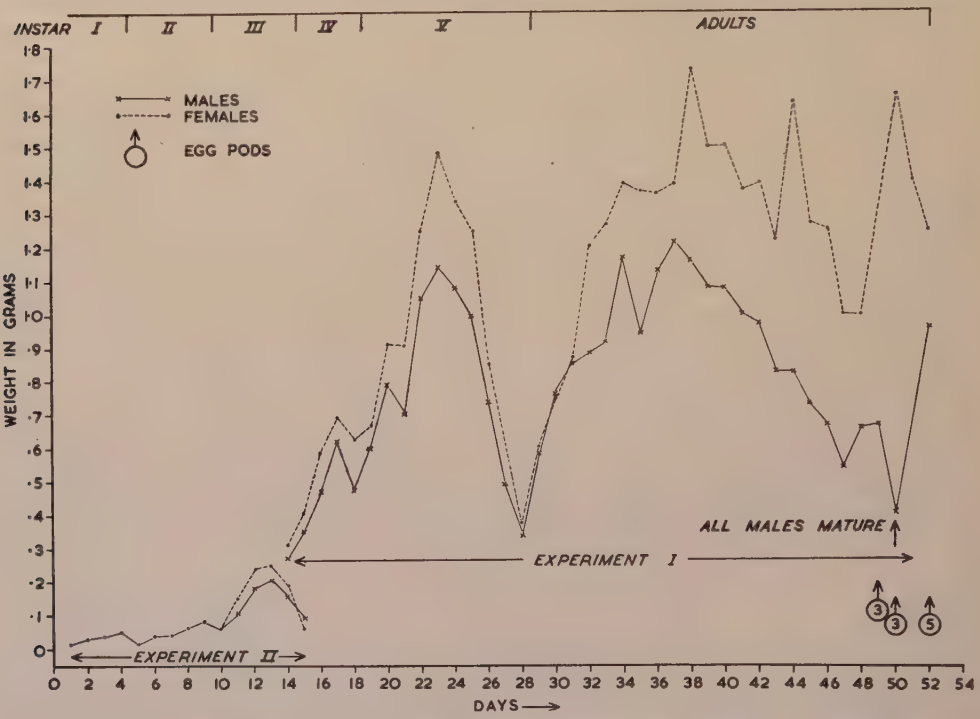


Fig. 3.—Average weight of fresh grass eaten by males and females of *Schistocerca gregaria* Forsk. on each day of their life-history. (Sexes not separated before instar III.)

The percentage of food assimilated by hoppers has been calculated from the dry faeces and the estimated dry weight of food eaten (fig. 1) and is as follows:—

Instar	I	II	III	IV	V
Percentage of food assimilated ..	78·2	51·5	45	34	35

The proportion of food utilised during development is small, as is to be expected (Weis-Fogh, 1952), and the youngest hoppers assimilate the most.

Effect of crowding on quantities eaten.

Since preliminary experiments had shown that hoppers kept in crowds ate more than those kept in groups of three in more confined conditions, a third series of first-instar hoppers were set up (Experiment III). This consisted of 12 groups, of 12 hoppers each, in large celluloid cylinders, and the same quantity of grass per hopper was provided as in Experiment II. This experiment was carried out for the first three days of the instar and the results are shown in fig. 2.

The consumption of food per unit body weight was distinctly greater in experiment III than in experiment II, which suggests that the food consumption per hopper increased with the number of hoppers per cage, and the space available to them, but the following points must be taken into consideration. Experiment III was conducted about a month later than Experiment II, and uncontrolled factors such as the length of daylight and the quality of the grass, and other unknown seasonal factors, may have affected the results. Also, the temperature gradient in the large celluloid cylinders was about 10°C. between the part nearest to the bulb and that farthest away, whereas in the small glass tubes and the small celluloid cylinders it was not so great. Further, the hoppers were extremely active when being caught for weighing in the large celluloid cylinders, whereas in the smaller receptacles it was not necessary to disturb them so much and their activity was therefore less. These factors may account for the greater food consumption per hopper in experiment III, but there is clearly a need for further study of the effects of numbers on food consumption.

The Weight of Wheat Bran Eaten by Hoppers.

In preliminary experiments, a proportion of first-instar hoppers did not feed when provided with wheat bran in the laboratory, which suggests that the hoppers may not always be effectively baited at this stage. On the other hand, fifth-instar hoppers generally all fed, provided they were not about to moult, so that poison bait would be quite effective against them if properly formulated and spread. The formulation depends on the size of meal eaten and the toxicity of the insecticide. As toxicity experiments are not allowed in the laboratory of the Anti-Locust Research Centre because of the danger to the main stocks of locusts, it was decided to obtain weights of bran meals alone.

The wheat bran used in these experiments was standard ' Coarse Millers Offal ' which comprises the husk of the grain plus an unspecified quantity of adhering endosperm. The husk (not to be confused with chaff, which is removed during threshing) consists of the pericarp, testa, nucellar layer and aleurone layer; within it lies the endosperm (Kent-Jones & Amos, 1947). The husk composition of grain is about 13 per cent.

Weights of bran meals eaten were obtained for each day of the fourth and fifth instars, but only for the third day of the first instar because of the difficulty of inducing first-instar hoppers to feed.

First-instar hoppers which had hatched overnight were fed on grass until the third morning after hatching. On that morning, fresh grass standing in water was placed in the cage for one hour. At the end of that time, while there was no guarantee that all the hoppers were at exactly the same state of repletion, there was reason to believe that most of them would have fed once. Thirty-eight weighed hoppers were individually provided with weighed bran in $1\frac{1}{4} \times 2\frac{1}{2}$-inch glass tubes for two hours. The faeces were then removed and the bran re-weighed. Fourth- and fifth-instar hoppers were given fresh grass 24 hours before the test, some of the grass still being available to them immediately before they were given wheat bran. Hoppers were weighed individually and placed in 1 lb. glass jars containing a weighed quantity of wheat bran at approximately the same time each day, and after two hours the hoppers and their faeces were removed from the wheat bran, which was then re-weighed. The temperature in each jar, as indicated by a mercury-bulb thermometer suspended in another jar, was about 30°C.

The first-instar hoppers were weighed on an aperiodic balance reading to 0·2 mg.; their bran meals were small and were weighed on a 10-mg. torsion balance reading to 0·02 mg. The fourth- and fifth-instar hoppers and their bran meals were weighed on an aperiodic balance reading to 2 mg.

The bran meals of the first-instar hoppers were weighed in the same conditions of temperature and humidity as those in which feeding took place because it was hoped to reduce errors due to the hygroscopic nature of the bran. Despite these precautions there were differences in weight between two weighings of bran upon which no hoppers had fed, and these were larger than would be accounted for by the errors of the balance. However, as they were only of the order of approximately 5 per cent. of the meal sizes, they were neglected in the presentation of the results. The bran meals of the fourth- and fifth-instar hoppers were weighed at a lower temperature than, and at humidities different from, those at which feeding took place, but errors were again only of the order of 5 per cent. of the weight of the meals.

The data obtained are shown in fig. 4. They show that wheat-bran meals are variable on all days of the fourth and fifth instars, but that, on the average, feeding is greater in the middle of each instar (*cf.* p. 542). They also show that the quantity eaten by hoppers on the third day of the first instar is approximately equivalent to that eaten per day just before and just after moulting by hoppers in the fourth and fifth instars. At these times, on four days of the seven of the fourth instar and on four days of the twelve of the fifth instar, most of the hoppers ate relatively small quantities of bran or did not eat at all.

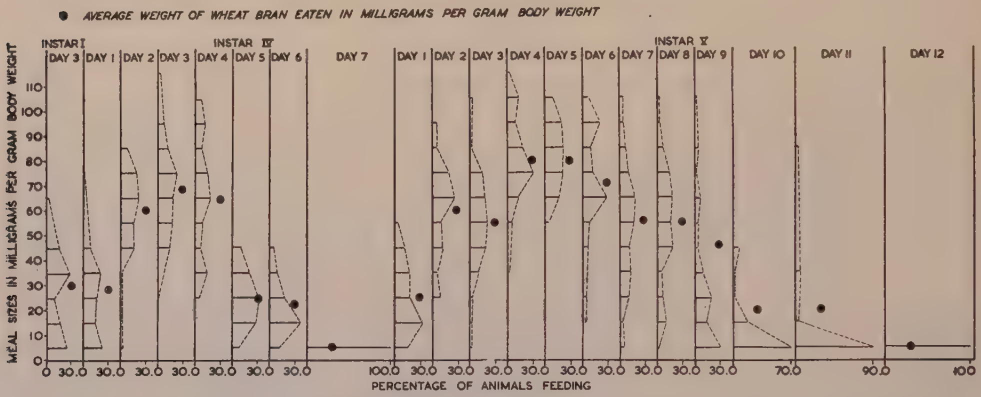


Fig. 4.—The frequency distribution of sizes of meal of wheat bran eaten by *Schistocerca* hoppers of instars I, IV and V during daily two-hour test periods.

Increase in Length and Weight of Hoppers and Weight of Adults.

At the same time as the hoppers were weighed during the experiments with wheat bran, their lengths from the apex of the head to the tip of abdomen were measured with a ruler to the nearest mm. The results are shown in figs. 5 & 6, which represent length and weight relationships. The three calculated lines of the formula $W = kL^3$, where W = weight in gm., k (a constant) = 0·01, 0·02 and 0·3 and L = length in cm., embrace nearly every point on the graph. This indicates that within broad limits the shape of the hopper is the same in each instar. The instars are plotted with alternate dots and crosses and show overlapping, but the small number of insects measured does not warrant a closer investigation into the increases in weight and in extension of the abdomen which take place within an instar . A comparison of figs. 5 and 6 shows that females tend to be heavier and larger than males in the fifth instar but not in the first. The females grow more rapidly than the males, as has been pointed out by Chauvin (1941) and Husain & Mathur (1944) (see Table I).

After the final moult, although considerable quantities of grass are eaten (fig. 3), the body weight increases only 1·4 times during 14 days, whereas during

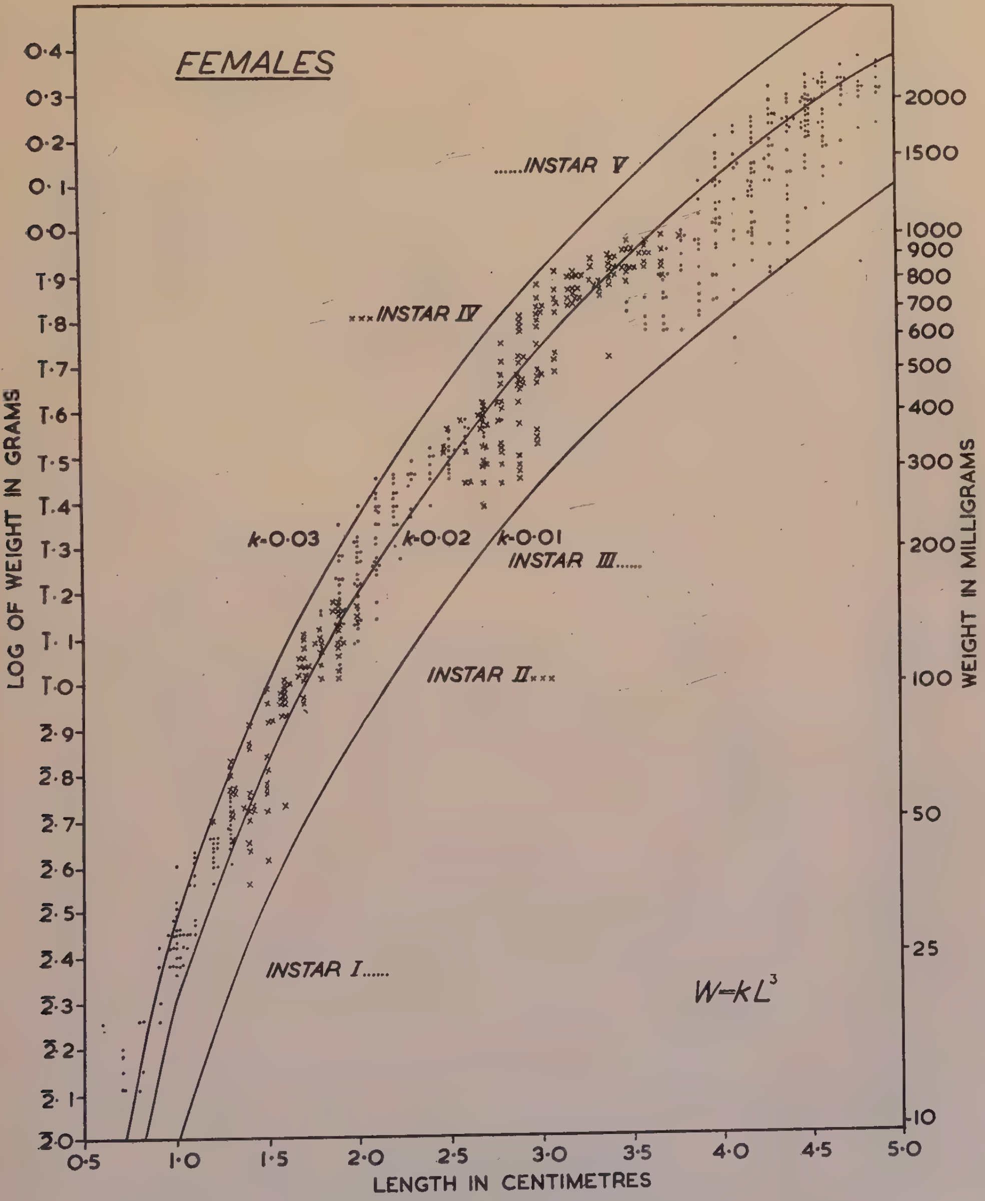


Fig. 5.—Growth in weight and length of females of *Schistocerca gregaria* Forsk.

the first 14 days of the hopper life the weight increases about 15 times and during the following 14 days about 4·5 times.

The average increase in weight of a series of adults obtained during January 1951 compared with that of about 20 male and 20 female adults of Experiment I,

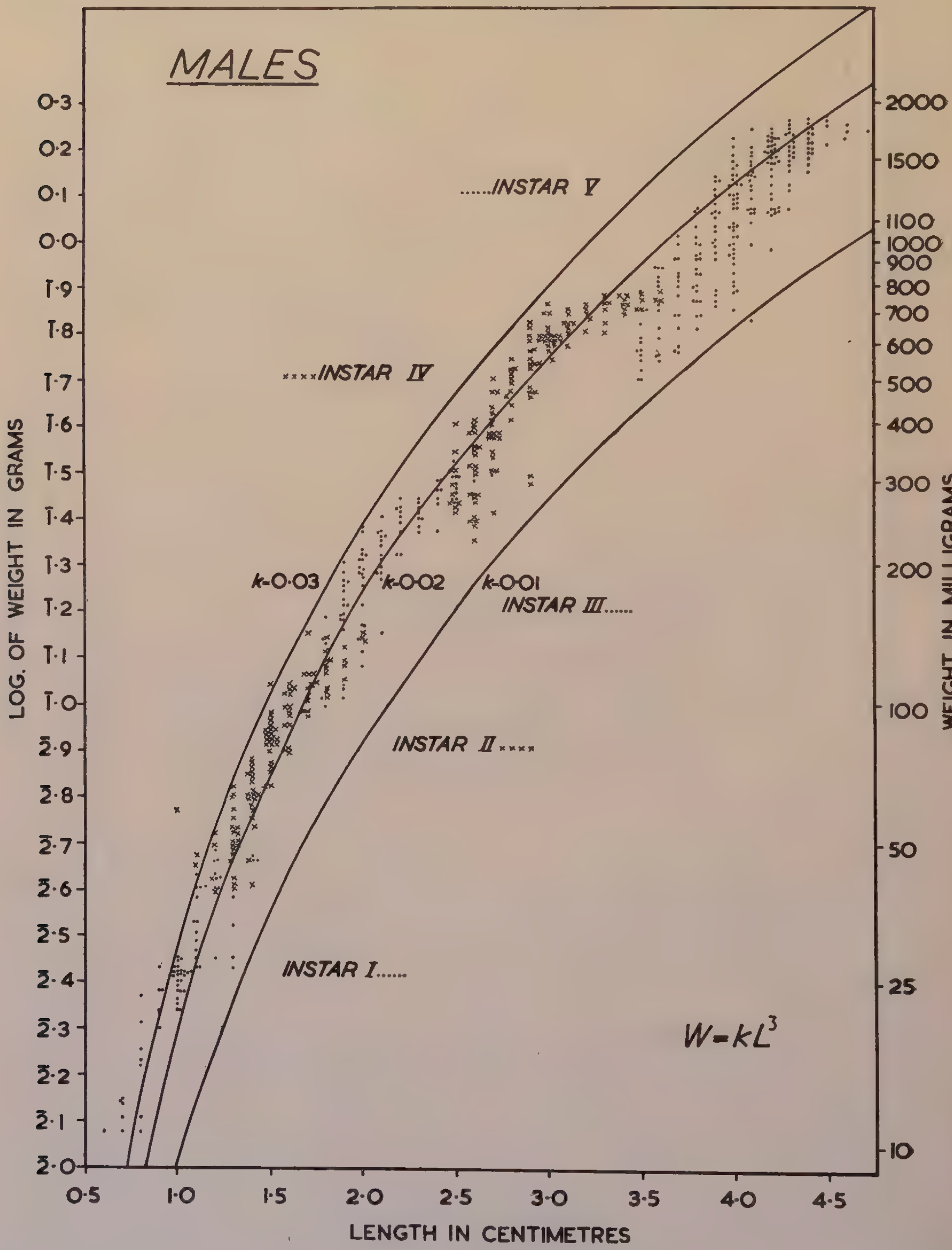


Fig. 6.—Growth in weight and length of males of *Schistocerca gregaria* Forsk.

TABLE I.

A comparison between the weights (in mg.) of *S. gregaria* hoppers and adults obtained by various workers.

Instar	Davey (present work)				Bodenheimer (1929)		Richards (1930) (*a*)		Karandikar (1933) (*b*)		Chauvin (1941) (*c*)			Husain & Mathur (1944)				Husain, Mathur & Roonwal (1949)
	♂♂	n	♀♀	n		n	Age	Mean weight	Lab'ry	Field	Age	♂♂	♀♀	♂♂	n	♀♀	n	
I Beginning	10–28 (18)	20	10–30 (18)	20	21·4–24·6 (23·2)	5	Hatchlings	(21)			1 day	25·1	23·5	(18·3)	13	(18·3)	10	26–38 (33)
Middle									(27)	(18)	3 days	31·3	31·9					
End	27–54 (40)	26	30–56 (46)	26			7 days	(29)										
II Beginning	40–64 (48)	21	44–49 (54)	18	46·3–50·2 (48·1)	5	10 days	(46)			6 days	40·6	36·3	(30·5)	10	(31·2)	9	73–81 (81)
Middle									(68)	(37)	8 days	50·3	70·1					
End	97–140 (120)	20	124–150 (138)	18														
III Beginning	90–184 (134)	22	110–184 (144)	25	90·2–200·7 (95·3)	5	14 days	(75)			12 days	93·8	105	(83)	9	(81·6)	5	117–214 (191)
Middle									(188)	(99)	14 days	103·5	117					
End	232–308 (274)	18	246–366 (314)	18			21 days	(215)										
IV Beginning	226–326 (272)	19	244–360 (306)	21	190–276·5 (231·1)	7					22 days	336·8	367·5	(220·7)	8	(252·7)	5	340–627 (429)
Middle									(401)	(278)	27 days	514·8	562·2					
End							28 days	(483)										
V Beginning	496–984 (702)	16	606–974 (762)	17	419–762 (528)	5					32 days	895·7	1022·4	(558·3)	9	(720·4)	4	737–1510 (950)
Middle									(1027)	(525)								
End	1282–1694 (1578)	20	1402–2342 (1832)	14			35 days	(1094)										
Adults Newly moulted fledglings	1152–1650 (1434)	20	1604–2160 (1816)	20	♂♂ 1038–1995 (1486)	5	37 days	(1380)	—	(1310) (1750)	42 days	1244	1597·3	(1307·2)	7	(1895·9)	5	
					♀♀ 2635–3115 (2882)	5												

The range of weight is given where available and the average (in brackets). Unless otherwise stated the authors arranged their data according to instars. n = number of individuals.

(*a*) The author does not indicate to which instar the hoppers belong. His results are given as hoppers per chhatak (58 gm.), from which the mean weights have been calculated.

(*b*) The author states for the laboratory experiments that the average weight of the hopper for each stage was calculated by taking the mean of the weights at the beginning and the end.

(*c*) The author carried out the weighings at irregular intervals. He gives the instars, but does not state the numbers of individuals on which the results were based.

carried out in October 1952 is shown in fig. 7. Fig. 7 also shows that the females continue to increase in weight after the males have become more or less static. However, because the points plotted are averages, the graph does not show either the loss in body weight of a female after an egg pod has been laid or the subsequent increase prior to the next egg-laying.

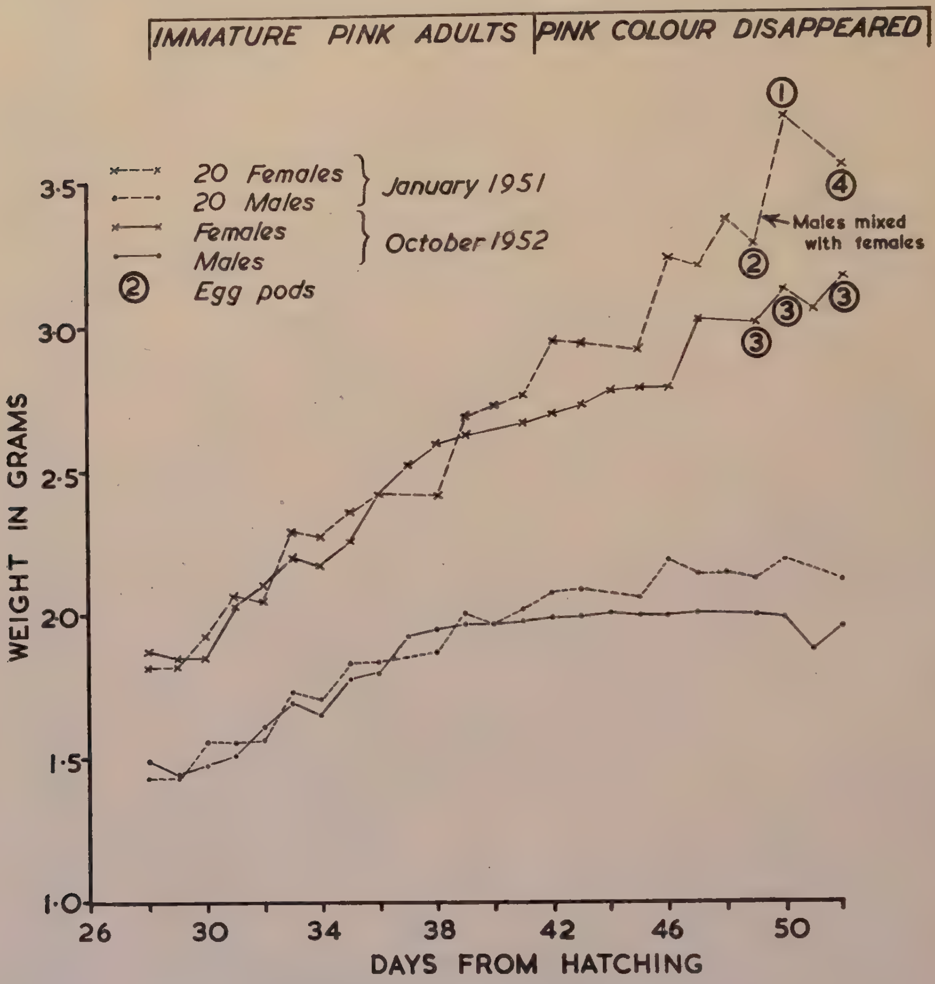


Fig. 7.—Average weight of male and female adults of *Schistocerca gregaraia* Forsk.

Discussion.

Attempts were made (Gunn, Perry & others, 1948) to estimate the quantity of adult locusts in a basking swarm; they concluded that one acre of land may contain about one ton of locusts. The average weight of a locust in a swarm was estimated from Bodenheimer (1929) to be 1·67 gm., and this figure agrees well with our weighted mean for 38 male fledglings weighing 56·01 gm. and 29 female fledglings weighing 53·72 gm., which is 1·66 gm. However, 20 days later, while the locusts were still maturing, the mean was 2·57 gm. (36 males weighing 72·54 gm. and 27 females 84·37 gm.), and this is about 1½ times their original weight. In order to reach this, the locusts consumed a mean of 22·6 gm. of fresh grass each (25–38 males ate an average of 17·79 gm. and 19–29 females ate an average of 27·44 gm.). Therefore a ton of fledglings would eat about 13·6 tons of fresh grass in increasing its weight by half.

The quantities of fresh grass eaten by hoppers of the various instars and adults in the laboratory show that all hoppers eat approximately the same relative quantity (one gram per gram body-weight) daily during the middle days of the instar, but adults eat half this quantity. The daily consumption of 0·5 gm. per gm. body-weight of adult is much smaller than that given by Weis-Fogh (1952) for a migrating swarm of adult locusts, which he says would require to eat at least one to one-and-a-half times its own weight every day and probably two or three times as much; but it must be remembered that the estimate of 0·5 gm. per gm. body-weight applies to caged adults which are not using up reserves of stored food during flight and would not therefore require to eat as much as migrating locusts.

Although hoppers of all instars ate approximately the same relative quantity of grass, the bran meals eaten by first-instar hoppers were smaller in relation to body-weight than were those of hoppers of the fourth and fifth instars. Experiments have shown that first-instar hoppers eat grass at a faster rate than bran and this may be due to the toughness of the bran as compared with grass, which may make the bran more difficult for the young hoppers to " approach or chew " (Clark, 1948). Preliminary experiments have shown that the Desert Locust cannot be reared beyond the third instar on wheat bran and water only; toughness of bran may partly account for this too, but it seems probable that some nutritional deficiency may also be involved.

The sizes of bran meals eaten in the laboratory (p. 543) suggest that a locust would ingest a median lethal dose of insecticide if this were mixed with the bran. Weinman & Decker (1949) give the median lethal dose of γ BHC for adults of *Melanoplus differentialis* (Thos.) as 6·6 μg per gm. body-weight. Standard bait contains 0·06 per cent. γ BHC; therefore the amount of bait for an LD-50 meal is 11 mg./gm. Assuming that similar figures apply to hoppers of *Schistocerca*, fig. 4 can be used to ascertain what proportion of a population of mixed ages will fail at any given opportunity to eat a meal containing a median lethal dose of insecticide. Over the 20 days of the life-history included in the test, a daily average of 24 per cent. of the hoppers did not eat a meal exceeding 10 mg./gm. body weight. This compares with the estimate of Ellis (1951) that 20 per cent. of a large population of fourth-instar hoppers of *Locusta* in different stages of development failed to take bait on a particular day.

Summary.

The weight of fresh grass eaten by *Schistocerca gregaria* (Forsk.) on each day of its development from hatching until maturation of the adults was investigated. Hoppers in all instars ate on the average about one gram per gram body-weight per day on the middle days of the instars and the adults ate approximately half-a-gram per gram body-weight each day. The percentage of food assimilated, calculated from the dry faeces and estimated dry weight of food eaten, falls from about 78 in the first to 35 in the fifth instar. There were some indication that the food consumption per hopper increases with the number of hoppers per cage.

The weight of wheat bran eaten by hoppers was also investigated. The amount eaten by hoppers on the middle day of the first instar is approximately the same, in relation to their body weight, as that eaten per day just before and just after moulting by those in the fourth and fifth instars. More is eaten in the middle of these instars.

Measurements of weights and lengths of males and females in the hopper instars and of the weights of adults showed that in the course of their development

females became progressively heavier and larger than males. The weight of a newly-hatched hopper is about 10 mg.; a female fledgling weighs about 2 gm. and a male 1·5 gm. Hoppers are approximately 1 cm. long on hatching, and males on reaching maturity are about 4·5 cm. long and females about 5·0 cm.

The weight of wheat bran eaten by hoppers of the first, fourth and fifth instars, respectively, during two hourly periods indicated that a daily average of 24 per cent. of such population would eat less than 10 mg. per gm. body weight and thus might not consume a median lethal dose of insecticide if mixed with it at the standard rate.

Acknowledgements.

I am indebted to Dr. B. P. Uvarov, C.M.G., F.R.S., Dr. D. L. Gunn and Dr. M. Norris for many helpful suggestions. My sincere thanks are also due to Dr. T. H. C. Taylor for criticising and editing the work, Mr. D. E. Davies for great help with the statistical side and Mr. P. Hunter-Jones and the laboratory staff of the Anti-Locust Research Centre for assistance of various kinds. I am also indebted to Miss J. E. Tomsett for redrawing the figures in a form suitable for publication.

References.

Bodenheimer, F. S. & Others (1929). Studien zur Epidemiologie, Ökologie u. Physiologie der afrikanischen Wanderheuschrecke (*Schistocerca gregaria* Forsk.)—Z. angew. Ent., **15**, pp. 435–557, 55 figs.

Brown, E. S. (1947). The distribution and vegetation of egg-laying sites of the Desert Locust (*Schistocerca gregaria* Forsk.) in Tripolitania in 1946.—Bull. Soc. Fouad Ent., **31**, pp. 287–306, 4 pls., 3 tables, 2 maps.

Chauvin, R. (1941). Contribution à l'étude physiologique du criquet pèlerin et du déterminisme des phénomènes grégaires.—Ann. Soc. ent. Fr., **110**, pp. 133–272, 23 figs.

Clark, E. J. (1948). Studies in the ecology of British grasshoppers.—Trans. R. ent. Soc. Lond., **99**, pp. 173–222, 1 fig.

Ellis, P. E. (1951). The marching behaviour of hoppers of the African Migratory Locust (*Locusta migratoria migratorioides* R. & F.) in the laboratory.—Anti-Locust Bull., no. 7, [4 +] 46 pp., 32 figs.

Gunn, D. L., Perry, F. C. & Others (1948). Behaviour of the Desert Locust (*Schistocerca gregaria* Forskål) in Kenya in relation to aircraft spraying.—Anti-Locust Bull., no. 3, [2 +] 70 pp., 8 pls., 21 figs.

Gunn, D. L. (1952). Field tests of dry baiting against the Desert Locust, *Schistocerca gregaria* (Forsk.).—Bull. ent. Res., **42**, pp. 675–690, 6 figs.

Husain, M. A. & Mathur, C. B. (1944). Studies in *Schistocerca gregaria* Forsk. XI. The influence of temperature on the growth in weight and size of the hoppers.—Indian J. Ent., **5**, pp. 107–115, 1 graph.

Husain, M. A., Mathur, C. B. & Roonwal, M. L. (1949). Studies on *Schistocerca gregaria* (Forskål). XIII. Food and feeding habits of the Desert Locust.—Indian J. Ent., **8**, (1946), pp. 141–163, 4 figs.

Karandikar, K. R. (1933). Annual report of the Locust Research Laboratory Pasni (Baluchistan), for the year 1932.—39 pp.—Simla, Govt. India Pr.

Kent-Jones, D. W. & Amos, A. J. (1947). Modern cereal chemistry.—4th edn., pp. 1–2; Liverpool, Northern Publ. Co.

Richards, P. B. (1930). Memorandum on locust control operations in the United Provinces.—*In* Locust control, pp. 12–60. Allahabad, Govt. Pr.

Weinman, C. J. & Decker, G. C. (1949). Chlorinated hydrocarbon insecticides used alone and in combinations for grasshopper control.—J. econ. Ent., **42,** 135–142, 1 graph.

Weis-Fogh, T. (1952). Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forskål).—Phil. Trans., (B), **237,** no. 640, 36 pp. 12 figs.

THE MELON STEM-BORER, *APOMECYNA BINUBILA* PASCOE (COLEOPTERA: LAMIINAE) IN THE SUDAN.

By D. G. Pollard, B.Sc.

Entomological Section, Research Division, Ministry of Agriculture, Sudan.

The larva of *Apomecyna binubila* Pasc. is an occasional though sometimes serious pest of sweet melon (*Cucumis melo*) and water melon (*Colocynthis citrullus*) in the Sudan. This same species is also a pest of cucurbits in South Africa (Fuller, 1914). Apart from short descriptions of the adult by Pascoe (1858) and Distant (1898, 1904) on South African material, and notes by King (1908, 1911) in the Sudan, there is no information available on the morphology or biology of the adult or immature stages of this insect. Fuller (*loc. cit.*) gives a brief account of the bionomics of *Apomecyna binubila* in South Africa and attention has been drawn, in this paper, to certain similarities and differences between the former account and the present observations made in the Sudan.

Specimens of all stages were obtained from melons in the Wad Medani area—from the Gezira Research Farm during 1950, and from riverain cultivations along the Blue Nile during 1952. Rearing was carried out in petri-dishes (6 cm. diameter) at temperatures ranging between 26·7–35·5°C. (80–96°F.) with an average of 30·6°C. (87°F.). Small sections of melon stem, renewed daily, were provided as food for the larvae. Larvae were preserved in Pampel's fluid; adults were dry-mounted or preserved in spirit.

Systematic Position.

Apomecyna.

Apomecyna Latreille: 1829, in Cuvier, Règne Anim., edn. 2, **5**, p. 126.
Serville: 1835, Ann. Soc. ent. Fr., **4**, p. 77.
Lacordaire: 1872, Gen. Coléopt., **9** (2) p. 580.

Mecynapus Thoms.: 1858, Archiv. Entomol., **2**, p. 187.

The genus is placed in the Division Apomecynini (Apomécynides, Lacordaire 1872; Apomecynidaria, Distant 1904) of the sub-family Lamiinae (Lamiidae) of the Cerambycidae.

Apomecyna binubila Pasc.

binubila Pascoe: 1858, Trans. ent. Soc. Lond., (2) **4**, p. 253.
Distant: 1898, Ann. Mag. Nat. Hist., (7) **1**, p. 372.

senegalensis Dej. MS. (Distant 1904).

Description of the Stages.

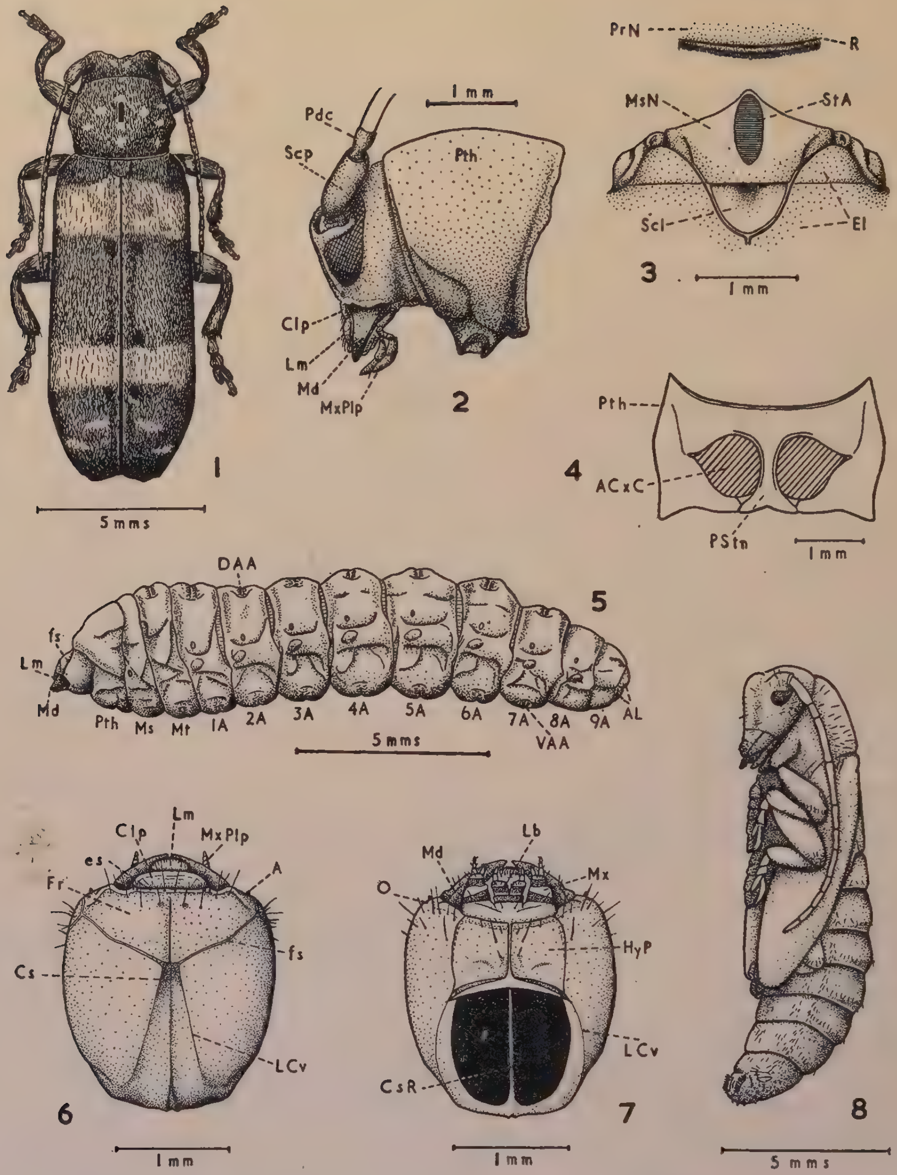
Egg.

The egg is elongate with rounded ends and one side a little less convex than the other. The chorion is opaque white and bears faint pentagonal markings. Size, 1·7 mm. × 0·5 mm.

Larva.

The size of the first-instar larva on hatching is 1·5 mm. × 0·5 mm.; abdomen and thorax are white, head brown.

The full-grown larva is cylindrical, tapering slightly anteriorly and posteriorly.


1
5 mms
Pdc
Scp
Pth
1 mm
Clp
Lm
Md
MxPlp
2
PrN
R
MsN
StA
Scl
El
3
1 mm
Pth
4
ACxC
PStn
1 mm
DAA
5
fs
Lm
Md
Pth
Ms
Mt
1A
2A
3A
4A
5A
6A
7A
8A
9A
AL
VAA
5 mms
Lm
Clp
MxPlp
es
A
Fr
fs
Cs
LCv
6
1 mm
Lb
Md
Mx
O
HyP
LCv
CsR
7
1 mm
8
5 mms

Figs. 1–8.—(1) adult; (2) head of adult, lateral aspect; (3) stridulating apparatus of adult; (4) prothorax of adult, ventral aspect; (5) larva; (6) head of larva, dorsal aspect; (7) head of larva, ventral aspect; (8) pupa. Abbreviations used: (A) antenna; (1A)–(9A) abdominal segments; (ACxC) anterior coxal cavity; (AL) anal lobes; (Clp) clypeus; (Cs) coronal suture; (CsR) coronal ridge; (DAA) dorsal ambulatory ampulla; (El) elytron; (es) epistomal suture; (Fr) frons; (fs) frontal suture; (HyP) hypostomal plate; (Lb) labium; (LCv) line of attachment of neck membrane; (Lm) labrum; (Md) mandible; (Ms) mesothorax; (MsN) mesonotum; (Mt) metathorax; (Mx) maxilla; (MxPlp) maxillary palp; (O) ocellus; (Pdc) pedicel of antenna; (PrN) pronotum; (PStn) prosternum; (Pth) prothorax; (R) ridge (of pronotum); (Scl) scutellum; (Scp) scape of antenna; (StA) striate stridulatory area; (VAA) ventral ambulatory ampulla.

The body is soft, white or whitish-yellow in colour becoming darker as the larva shrinks prior to pupation. A sparse covering of thin yellow setae invests the body. Average length is about 17 mm. but there is much variation in size and this is apparently related to food supply during the larval period.

Head depressed, longer than broad, with sides converging posteriorly and not parallel in anterior and middle regions. Anterior exposed part more heavily sclerotised than the posterior section which is invaginated into the prothorax. Coronal suture continuing up to the epistoma (internally it forms a pronounced ridge in the posterior region of the head capsule). Epistomal region and mandibles heavily sclerotised; six epistomal setae present. Mandibles bearing a short slightly curved cutting edge and an inward tooth apically; proximally the molar area is indistinct and very weakly ridged. Outer surface black, shining, and bearing two setae. Labrum and clypeus large; maxillary palpi three-segmented.

Antennae three-segmented with the first segment longest and third shortest; segment 2 bearing a small supplementary segment in addition to the third. Ocelli slightly protuberant and close to, but separate from, the antennae. Occipital foramen in posterior ventral region of the head capsule. Mid-ventral area of capsule bridged by a pair of large hypostomal plates.

Legs absent; metathoracic and abdominal segments 1–7 with dorsal and ventral tuberculate ampullae. Abdominal segment 9 unarmed; segment 10 small with three shallow lobes (one dorsal, two latero-ventral) surrounding the anus.

Pupa.

Soft-bodied, exarate; yellow to yellow-brown at first, darkening later. Length, 13 mm.

Head with long, stiff, brown setae sparsely distributed on labrum, frons, vertex and genae; denser covering of very short brown setae on vertex and pronotum.

Abdominal terga 1–6 bearing transverse bands of long and short yellow-brown setae near posterior borders. Anterior borders of same terga with acute sclerotised spines, brown with black tips. Spines sparse and small on anterior terga, increasing in size and in number posteriorly and continued onto segments 7 and 8 where they cover the whole tergum. Segments 2–8 with lateral tufts of long setae. Segment 9 with two oblique rows of dark-brown capitate setae surrounding terminal segment and anus.

Femora and tarsi, bearing small tufts of long setae.

Adult.

Form elongate, slightly depressed. Colour dark brown, shining, covered by dense white and yellow-brown decumbent pubescence; finely and coarsely punctured. The underlying dark brown body colour gives a grey appearance to areas covered by white pubescence and a dark yellow-brown appearance to regions overlaid by the yellow-brown hairs. Length, 10 mm.–12·5 mm. (These figures are for specimens captured in the field; individuals as small as 7·0 mm. can be obtained by withholding food during the larval stage.)

Head.—Hypognathous, fitting closely into prothorax. Eyes of medium size, anterior edges emarginate and nearly divided by the antennal bases. Head, including labrum and clypeus, finely punctured, with large deep punctures on frons, vertex, and genae.

Antennae filiform, arising from short tubercles on front of head and extending two-thirds the length of body; 11-segmented. Segment 1 (scape) and to a lesser extent segment 2 (pedicel) with a proximal constriction; the scape three times as long as the pedicel, this latter the shortest segment in the antenna. Third and fourth segments equal, longer than all other segments except the scape. Segments 5–10 shorter than 3 and 4, becoming progressively smaller towards the apex except for the terminal segment (11) which is equal to segment 5. Average measurements of the antennal segments, in millimetres, are: 1 (1·22), 2 (0·41), 3 (1·02), 4 (1·01), 5 (0·58), 6 (0·54), 7 (0·54), 8 (0·50), 9 (0·48), 10 (0·44), 11 (0·59). The antennal segments have a yellow-white pubescence, replaced by white at the proximal and distal rims.

Mandibles strong, curved, shining, finely punctured except at apex, with two sharp-pointed black teeth. Slight yellow-brown pubescence present on the outer proximal mandibular face.

Thorax.—Prothorax nearly circular in transverse section; wider than long; sides slightly protuberant near middle; anterior and posterior edges of pronotum margined. Prosternum extending a short distance beyond the anterior coxae and produced laterally behind them. Prothorax pubescent, mainly yellow-brown but with small patches of white; deeply punctured.

Scutellum small with hind margin rounded and anterior surface, in mid-line, depressed; clothed with white and yellow-brown hairs; finely punctured. Mesonotum bearing an oval-shaped raised area covered with minute transverse striae (in stridulation, these striae are rasped by a thin sharp ridge running along the inside of the posterior margin of the pronotum).

Elytra are broader than the thorax and covered by yellow-brown pubescence except for two large transverse patches of white, one near the base, the other near the apex. Finely punctured, with 10 irregular longitudinal rows of coarse deep punctures which just show through the pubescence. Lateral and median edges margined, the former nearly parallel but tapering and truncate posteriorly where the elytra overlap the abdomen. Shoulders scarcely protuberant.

Hind wings with venation of Cantharid type showing the fusion of M1 and M2 towards the margin.

Legs pubescent, mainly brown but with small patches of white; finely and coarsely punctured. Anterior coxae globular, the coxal cavities not contiguous. Femora are dilated on the distal side of the centre; anterior tibiae with shallow slanting groove on inner side; tarsus with 4th segment reduced and 3rd strongly bilobed.

Abdomen.—Yellow-brown pubescence with spots of white; coarse punctures principally in lateral regions of sternites.

Distribution.

Apomecyna has a wide distribution occurring in the Ethiopian Region (Sudan, Tanganyika, Congo, South Africa), Oriental (India, Ceylon, Burma, China, Philippines), Australasian (Queensland) and Neotropical (Chile) Regions.

Aurivillius (1922) lists 25 Ethiopian species of *Apomecyna* to which must be added three species subsequently described. Of these, six species have been recorded from the Sudan, *viz.*, *A. binubila* Pasc., *A. cavifrons* Thoms., *A. latefasciata* Qued., *A. scalaris* Serv., *A. klugi* Thoms., and *A. parumpunctata* Chevr. (= *longipennis* (Thoms.)). Only *A. binubila* Pasc. is of importance as a pest.

In the Sudan, *Apomecyna binubila* has been recorded only between the 12° and 20° parallels of latitude. The following list shows the localities from which it has been taken; initial records only are given.

Nile: Letti Basin, iv.1916, (H. H. King); Nyambe Basin, 26.v.1911, (H. H. King); Affat, 15.v.1915, (H. H. King); Shendi, 1.iii.1923, (W. E. Giffard); Shambat, iii.1908, (?); Khartoum, 20.iii.1922, (H. H. King).

Blue Nile and tributaries: Rufaa, iii.1904, (A. Balfour); Wad Shafi, 1940, (H. N. Ashford); Wad Medani, iv.1925, (H. W. Bedford); Dinder, 13.iii.1929, (A. M. Makkawi).

White Nile: El Geteina, 19.iii.1928, (H. B. Johnston).

Kordofan: Bara, 7.ii.1951, (D. G. Pollard).

Darfur: Zurri, 4.iv.1915, (H. H. King); Kulme, 6.vii.1921, (H. Lynes).

Red Sea Hills: Khor Arbaat Delta, iv.1926, (H. B. Johnston).

It is probable that this list could be considerably extended, particularly in the melon-growing regions of Kordofan and Darfur.

Life-History and Habits.

Most Cerambycids are wood-borers characterised by the long duration of the larval stage: two to three years is common, up to 20 years has been recorded (Duffy, 1952). *A. binubila* is distinctive in having a very short developmental period: in the Sudan, the period from oviposition to adult emergence occupies about 35 days. This is an adaptation essential for survival in a comparatively short-lived herbaceous plant.

Habitat.

The entire larval and pupal stages and a short part of the adult life is passed within the stem and petiole of melons. Highest infestation, and greatest damage, occurs at the base of the stem. *Apomecyna* appears to have no direct competitors in this habitat; indirectly it may be affected by other melon pests such as larvae of *Rhaphidopalpa foveicollis* (Luc.) (GALERUCIDAE) and adults and nymphs of *Aspongopus viduatus* (F.) (PENTATOMIDAE) both of which are capable of destroying plants with great rapidity.

Oviposition.

Site.—Eggs are deposited singly, mainly in the internodes, sometimes in nodes, but only occasionally in petioles. They are either inserted in the tissues—when they may lie parallel to the axis of the stem or at right angles to it—or in the central hollow fistular pith. Fuller (*loc. cit.*) failed to find eggs in this latter position: in the Sudan they have frequently been found but only in the narrow stems of very young plants. Eggs in this position are held in place by fine adhering strands of pith. In older plants with thick woody stems, particularly water melons, the eggs are placed just below the thin bark layer and held in position by pressure of the tissues. In all cases, eggs are deposited only one to two millimetres below the external surface of the plant.

Method of insertion.—Oviposition has not been observed. The head of the adult, with flattened frons, powerful mandibles, and antennae inserted high on the face, is adapted for gnawing slits in the bark (fig. 2), (see Trägårdh, 1930). However, the proximity of eggs to the outer surface of the plant, the very small hole which is made for egg insertion, and the softness of the tissues in which eggs are laid, strongly suggests that insertion is performed only by the ovipositor and that the mandibles are not used for preliminary piercing of the stem. Eggs have not been observed in growth cracks or scars as reported for *A. histrio* (F.) (May, 1946).

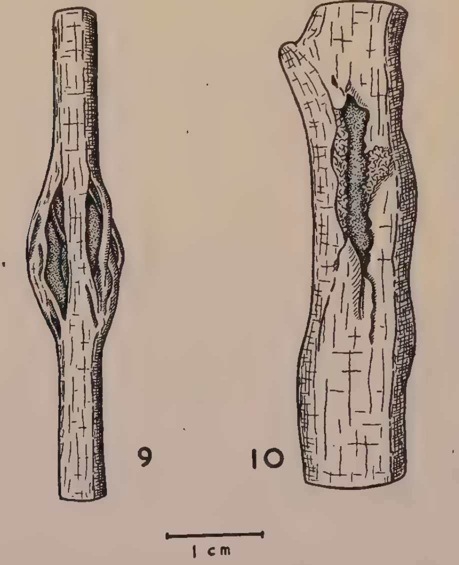
Reaction of plant tissue.—The hole formed during oviposition is rapidly filled by a sticky exudate from the plant. This oozes out and hardens to form a dark brown shining globule covering the external aperture of the hole, thus sealing the eggs off from the exterior. The exudate results from mechanical penetration of the stem and can be simulated by puncturing with a needle. It appears to originate from the cortex. Where eggs are laid in the fistular pith, the exudate may also escape into and line the interior of the stem. On young green stems the straw-coloured discoloration associated with the oviposition site and noted by Fuller (*loc. cit.*) has been observed. On older stems the tissue surrounding the egg is darker.

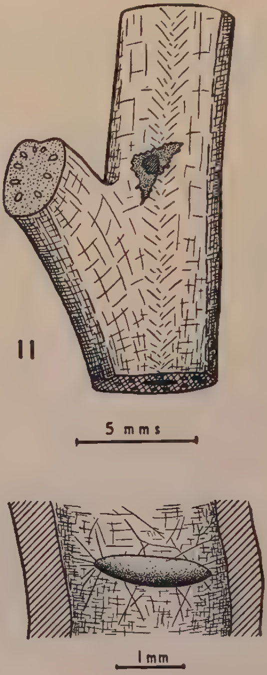
Incubation and hatching.—Eggs were collected in the field and allowed to hatch in the laboratory, the longest incubation period found being 4 days. The first-instar larva hatches by making a longitudinal slit extending three-quarters or more down one side of the egg.

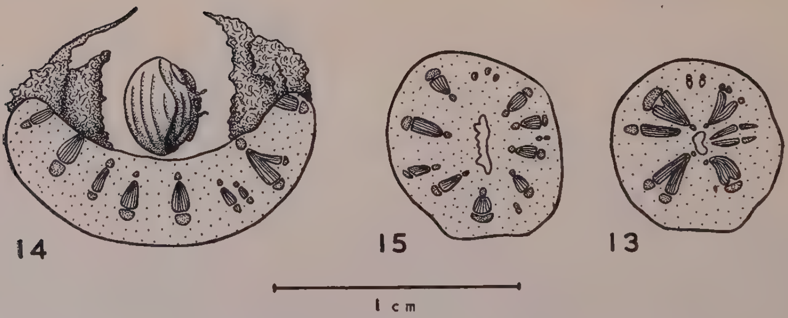
Larva.

The position of the larval tunnel is influenced by the girth of the stem. Where the latter is small and the egg is deposited in the central hollow, the larva tends to confine its tunnel to this region, consuming the green inner cortex. In older plants where the egg is placed below the bark, the young larva forms its tunnel between the bark and wood but usually extends the excavation into and along the wood, as it matures.

The length of an individual tunnel, of a mature larva, varies from 5 to 7 cm. and is widest (0·6–0·8 cm.) at the site of pupation. In thick woody stems, numerous parallel tunnels occur, which may join or overlap at their extremities. Up to 14 larvae and pupae have been found in a piece of stem 10 cm. in length by 2 cm. diameter.







Figs. 9–10.—Larval damage to melon stems: (9) knot-like swelling; (10) splitting with extrusion of frass.

Figs. 11–12.—The egg: (11) oviposition site covered by plant exudate; (12) egg *in situ* in narrow stem.

Figs. 13–15.—Continuity of vascular tissues across a damaged region: (13) stem 4 cm. below site of pupation, T.S.; (14) stem at the site of pupation, T.S.; (15) stem 4 cm. above the site of pupation, T.S.

There is no definite evidence of larvae constructing exit-holes to the exterior prior to pupation. In view of the extensive splitting and cracking of stems which usually occurs, such constructions would be largely superfluous. A stem may occasionally be found with the outer surface intact; in such cases, however, the internal tissues have been completely destroyed by a high larval population, leaving only a very thin outer rind for protection of the pupae. A similar observation is made by Fuller (*loc. cit.*).

Frass pellets, which are green in young stems, or brown in old woody tissues, are produced by the larvae and line the interior of the burrows, becoming exposed if the stem is cracked or split. The frass also becomes compacted at the extremities of the burrows and may thus cut off the originally continuous tunnels of different larvae.

The larval stages, under laboratory conditions, occupy 22 to 29 days with an average period of 25 days. There appear to be six larval instars, but this point requires further investigation.

Pupa.

The mature larva becomes quiescent and remains inactive and non-feeding for two to four days before pupating. A slight diminution in size, by 10–15 per cent. occurs and the colour darkens slightly, becoming more yellow. Pupation occurs near to the centre of the larval tunnel, the pupa lying parallel to the axis of the stem. There is little attempt at constructing a cocoon, beyond compacting the frass along the sides and at the extremities of the burrow and frequently, when the stem is split, the pupa is exposed to the exterior. The cocoon would thus appear to be even more fragile than that described by Fuller (*loc. cit.*) in South Africa.

The pupal period varies from 4 to 8 days with an average of 5·9. This agrees closely with the figure of 6 days quoted by King (1908).

The pupa displays considerable activity, jerking movements of the abdomen being evinced on the slightest disturbance. During the pupal period the colour deepens from yellow to yellow-brown.

Adult.

Emergence of the adult requires about 15 minutes. A split appears in the pupal skin above the vertex of the head and the skin is steadily propelled backwards. The adult is pale fawn in colour after emergence; pigmentation develops and in about 48 hours the typical adult coloration is complete.

Fuller (*loc. cit.*) records the presence of adults resting in the dead dry stems of pumpkins: this resting stage also occurs in the Sudan but appears to be seldom of more than four to five days' duration, whereas Fuller reports a resting stage lasting over the winter period. Little is known of the seasonal history of *Apomecyna* in the Sudan; in the Wad Medani area, where melons are allowed to grow continuously in riverain cultivations, all stages can be found at all periods of the year. Under these conditions, a resting stage is not essential for survival. This probably applies to other riverain melon-growing areas, but the manner in which the insect survives the dry season in regions remote from the river is unknown. Possibly—in Kordofan for example—it can only survive in localities with a permanent water supply, and not on rain-cultivated crops.

The adult is an inactive insect which seldom takes wing and either feigns death, or stridulates, on being disturbed.

Host-Plants.

Apomecyna binubila is selective in its choice of host-plants, the larvae having been found only on sweet and water melons. Fuller (*loc. cit.*) records pumpkin (*Cucurbita maxima*) as an additional host in South Africa. There is a single record for the Sudan, of adults being found on vegetable marrow (*Cucurbita pepo*) but no evidence of larvae, or of feeding by the adults. Two records exist of an adult being taken on the sunt tree (*Acacia arabica*) but there are no records of larvae and it is unknown if sunt plays any part in the life of the insect. Attempts to induce adults to feed, in captivity, on sunt flowers and foliage were unsuccessful; they will however, feed readily on flowers and foliage of melons.

Damage.

The damage resulting from egg-laying is small and localised; likewise that inflicted by the adults in feeding on the foliage. Larval damage however, may be extensive. Externally it is shown in the splitting, cracking and discoloration of stems with extrusion of frass and dying off of leaves. Where the larval infestation is high (five or more per 10 cm. of stem) the internal tissues become riddled with frass-filled tunnels, the vascular bundles are interrupted and the plant dies. On young plants where the larval population tends to be lower (two–three per 10 cm. of stem) the tunnels occur mainly in the central fistular pith, and the larvae feed on the inner cortex. The stem continues to grow, but splits and swells at the site of pupation, often exposing the central hollow to the exterior. Examination of numerous such cases has shown, however, that the vascular tissues are not seriously interrupted and the plant is able to continue growth and bear fruit. An example of this is shown in figs. 13–15; the internal phloem and part of the xylem in a few bundles only have been destroyed at the site of pupation although the stem is split and to outward appearances heavily damaged.

The death of plants bearing small larval populations does occur but careful examination usually reveals larvae of *Rhaphidopalpa foveicollis* burrowing in the roots. These larvae, though much smaller than *Apomecyna*, inflict serious damage since they sever the vascular bundles, in addition to destroying other tissues, in the root.

A few cases only have been seen of *Apomecyna* larvae in the petioles and in the main tap root. None has been observed in the roots of plants growing in heavy clay (Gezira " cotton soil ") but only in plants grown on fine sandy river silt.

In the absence of larvae, *Rhaphidopalpa* damage can be identified by the small holes bored into the roots from the exterior; *Apomecyna* damage is seldom found below ground level and the tunnels are mainly larger and confined to the interior of the plant.

A Parasite of the Larva.

A number of pupal cocoons of *Iphiaulax* sp. (BRACONIDAE) has been found in melon stems, and in one case a larva, which subsequently pupated and emerged, was found feeding on a moribund larva of *Apomecyna binubila*. The rate of parasitism is low; examination of a large quantity of plant material yielded 251 *Apomecyna* larvae, pupae and adults, and 6 pupal cocoons of *Iphiaulax* sp. *i.e.*, a ratio of 1:42, or 2·4 per cent.

Summary.

The larva of *Apomecyna binubila* Pasc. is a stem-borer of cucurbits in South Africa and the Sudan. In the latter country its known distribution lies between the 12° and 20° parallels of latitude. A description of the morphology of adult, larva and pupa is given. Observations on the life-history reveal a very short developmental period of approximately 35 days from oviposition to adult emergence. The host range is restricted to sweet and water melon. Damage is only serious where larval populations are high and the vascular tissues are

destroyed. With smaller infestations (two to three larvae per 10 cm. of stem) vascular continuity is not seriously interrupted. Reference is made to *Iphiaulax* sp. (BRACONIDAE), the first record of a parasite from this beetle. The larva is parasitic on larvae of *Apomecyna.*

Acknowledgement.

The writer is indebted to Mr. R. C. Maxwell-Darling, Chief of the Research Division, for permission to publish this paper.

References.

AURIVILLIUS, C. (1922). Cerambycidae: Lamiinae I.—Coleopt. Cat., pt. 73, 322 pp. Berlin, Junk.

CRAIGHEAD, F. C. (1923). North American Cerambycid larvae. A classification and the biology of North American Cerambycid larvae.—Bull. Dep. Agric. Can., N.S. no. 27, 238 pp.

DISTANT, W. L. (1898). Coleoptera collected in the Transvaal.—Ann. Mag. nat. Hist., (7) **1**, pp. 366–378.

DISTANT, W. L. (1904). Insecta Transvaaliensia, **1**, pp. 148–9. London, the Author.

DUFFY, E. A. J. (1952). Handbooks for the identification of British insects. Vol. 5, pt. 12. Coleoptera (Cerambycidae). Keys to genera and species.—18 pp. London, R. ent. Soc.

FULLER, C. (1914). The Pumpkin Stem-borer (*Apomecyna binubila*, Pasc.).—Agric. J. Un. S. Afr., **8**, pp. 240–242.

KING, H. H. (1908). Report on economic entomology.—3rd Rep. Wellcome trop. Res. Lab., pp. 201–248.

KING, H. H. (1911). Report of the Entomological Section.—4th Rep. Wellcome trop. Res. Lab., pp. 95–150.

MAY, A. W. S. (1946). Pests of cucurbit crops.—Qd agric. J., **62**, pp. 137–150.

PASCOE, F. P. (1858). On new genera and species of Longicorn Coleoptera. Part III.—Trans. ent. Soc. Lond., (2) **4**, pp. 236–266.

TRÄGÅRDH, I. (1930). Some aspects in the biology of Longicorn beetles.—Bull. ent. Res., **21**, pp. 1–8.

GLOSSINA PALPALIS FUSCIPES NEWST. IN LAKE-SIDE AND IN RIVERINE FOREST.

By J. P. Glasgow.

East African Tsetse and Trypanosomiasis Research and Reclamation Organisation.

In 1944 a field station was opened near Port Victoria, on the eastern shore of Berkeley Bay, in the north-east corner of Lake Victoria (see fig. 1). The purpose of the station was to try out two possible methods of eradicating *Glossina palpalis fuscipes* Newst. along the lake shore. The first method tried was that of sheer clearing a very narrow strip nearest the water's edge. The strip cleared was at first only 100 feet wide, but this was later increased to about 100 yards by the

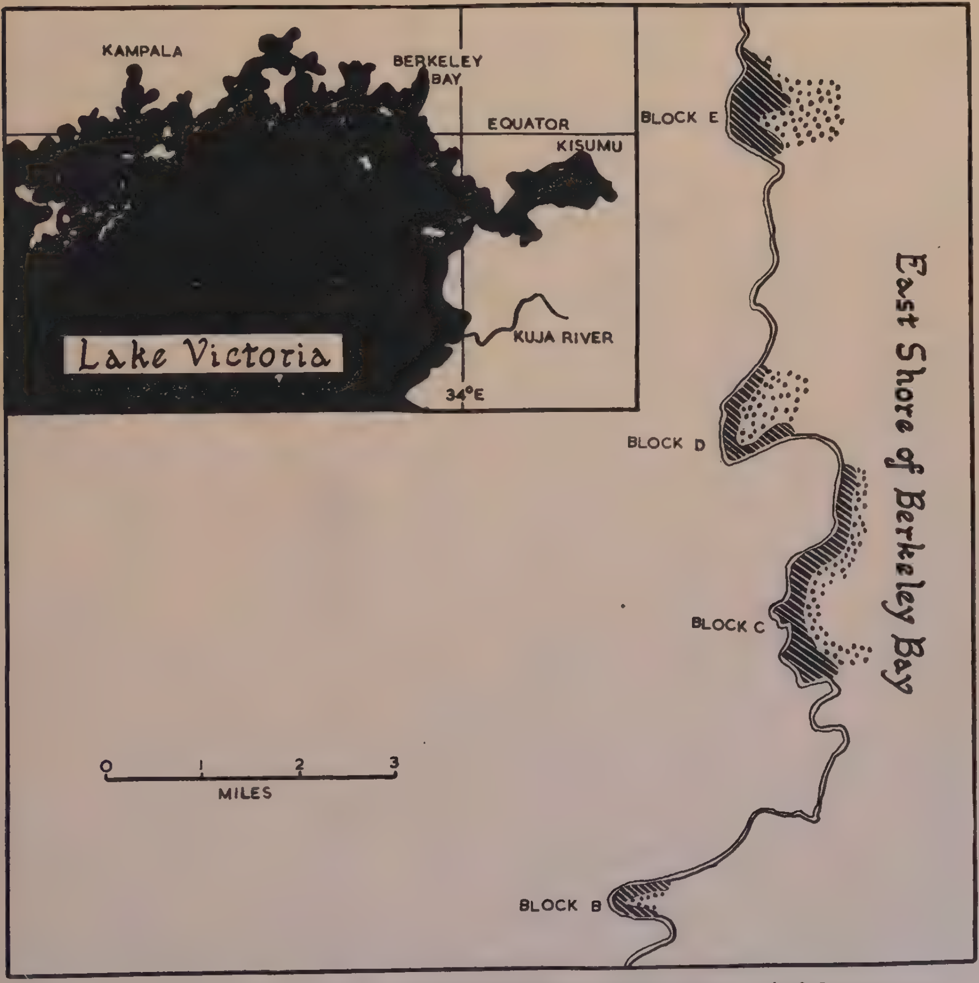

KAMPALA
BERKELEY BAY
EQUATOR
KISUMU
Lake Victoria
KUJA RIVER
34°E
BLOCK E
BLOCK D
BLOCK C
BLOCK B
East Shore of Berkeley Bay
0
1
2
3
MILES

Fig. 1.—Map of Berkeley Bay: black-white hatched, lake-side forest; stippled, evergreen thicket; inset, north-east corner of Lake Victoria.

removal of all the lake-side forest. This did not lead to the eradication of *G. palpalis*, because this fly is not so closely bound to the water's edge as had been supposed. It continued to live in appreciable although reduced numbers in the evergreen thicket which had been behind the original forest, and it became evident that clearing operations, to be successful against this tsetse, must be carried back some two or three hundred yards from the lake. The second experiment was originally to have been hand-catching, but after experience with this method in riverine forest (Glasgow & Duffy, 1951) the programme was changed. Partial clearing (undergrowth removal) was tried instead, as a possible method of reducing the cost of treatment, since the first experiment had shown that the areas to be treated were necessarily large. Undergrowth removal was found to be not cheaper, and less satisfactory than sheer clearing, because regeneration took place so rapidly in the shade of the large trees which were left standing that a suitable habitat for *G. palpalis* was reconstituted in only a few months.

Before and during the course of these experiments some observations of more general interest were made, and these are recorded in the present paper.

The experimental area was that used by Symes & Southby (1938) in their attack on lake-side *G. palpalis* by hand-catching. It was only necessary to clean up, and in one case extend, their large clearings to isolate two large experimental blocks and the control (block B). The experimental blocks were blocks C and D (narrow sheer clearing) and block E (undergrowth removal).

TABLE I.

Stevenson screen readings behind block D.

	Temperature		Saturation deficit at 2 p.m.
	Daily maximum	Daily minimum	
	Mean	Mean	Mean
1948			
November	87·0	57·8	20
December	87·2	63·6	22
1949			
January	88·3	65·2	19
February	85·7	62·7	20
March	88·3	64·5	18
April	84·1	63·6	13
May	82·1	63·5	15
June	82·2	61·5	11
July	81·5	61·1	11
August	81·9	62·0	12
September	82·8	62·6	16
October	—	—	—
November	—	—	—
December	—	—	—
1950			
January	87·4	67·0	—
February	86·0	—	—
March	85·2	—	16
April	83·2	—	12
May	82·5	62·7	13
June	82·2	61·2	13
July	81·8	59·8	14
August	85·1	60·7	13
September	82·1	61·8	14
October	85·0	60·7	18
November	85·8	61·2	17
December	86·1	60·9	20

Temperatures in degrees Fahrenheit, saturation deficits in millibars.

Climate.

Because of the presence of Lake Victoria, the climate is equable, and more like a coastal climate than what would be expected in the interior of a continent. The Stevenson screen readings made at our camp, which was behind block D are summarised in Table I. The screen was about 200 yards from the edge of the lake, on a plateau some 50 feet above lake level. It was in a clearing in the dense evergreen thicket which grew behind the lake-side forest. These readings do not represent the exact climate in which *G. palpalis* was living, which would be in general somewhat moister and more equable than that recorded, but they may serve for comparison with other places. Rainfall records are given in Table II. During the five years 1946–50 the annual total varied from 32 to 59 inches, with a mean of 41 inches. The driest months were January and February, and the wettest April and May, but the distribution as well as the total amount of rain varied considerably from year to year.

TABLE II.

Rainfall recorded at Lukala.

	1946		1947		1948		1949		1950	
	Ins.	Days	Ins.	Days	Ins.	Days	Ins.	Days	Ins.	Days
January	·0	0	5·95	9	·83	3	·45	3	1·64	5
February	·0	0	3·07	7	·80	7	·83	5	1·51	4
March	2·31	8	5·36	14	4·24	16	·55	6	8·21	13
April	10·41	17	12·37	18	4·45	15	6·32	18	5·39	7
May	5·78	13	14·01	20	4·92	21	5·43	14	4·70	14
June	3·08	12	4·32	11	2·79	13	3·01	8	3·05	9
July	1·03	7	2·72	13	2·91	10	1·58	10	0·93	5
August	5·88	14	·92	12	2·32	15	3·46	14	2·93	3
September ..	2·12	12	1·11	12	3·51	17	0·84	7	2·07	8
October	3·16	17	2·81	10	3·72	18	4·00	7	4·66	7
November ..	8·11	16	2·63	10	2·22	13	2·83	8	0·13	2
December ..	2·66	11	3·77	6	1·20	10	3·01	7	0·91	5
	44·54	127	59·04	142	33·91	158	32·31	107	36·13	82

Vegetation.

All the blocks consisted of lake-side forest, appearing from the water as a fringe of dense dark trees some sixty feet tall. The width of the forest varied greatly and depended on the topography, as is shown in fig. 2. Block B was on the side of a hill, and the forest fringe was little more than a single row of *Ficus vogelii* a tree not found in any of the other blocks. At the other extreme, in block E, there was a strip of flat ground about a hundred yards wide, only slightly above the level of the lake, and this flat was covered with a rich and varied tree growth. Actual counts of trees were made only in blocks C and D; these are given in Table III. Except in block B, the forest was less than 50 years old. This is shown by ditches and hippopotamus traps on the ground, and by the testimony of several elderly natives. This coast was much more densely inhabited before 1905; depopulation was associated with the epidemic of sleeping sickness at about that time. Block B is too steep and rocky ever to have been cultivated, and this forest may therefore be much older, although the evidence for this is not conclusive.

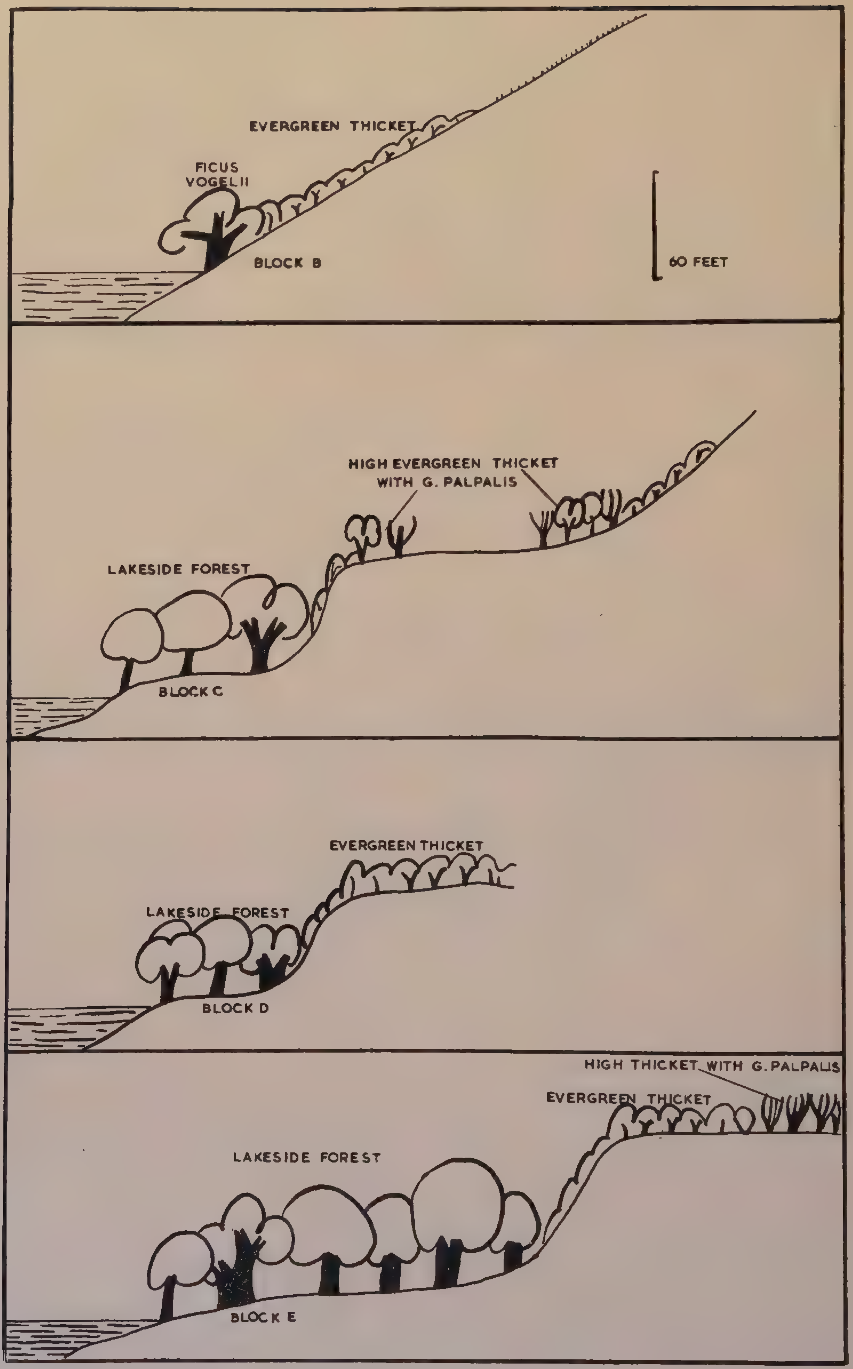

EVERGREEN THICKET
FICUS VOGELII
BLOCK B
60 FEET
HIGH EVERGREEN THICKET WITH G. PALPALIS
LAKESIDE FOREST
BLOCK C
EVERGREEN THICKET
LAKESIDE FOREST
BLOCK D
HIGH THICKET WITH G. PALPALIS
EVERGREEN THICKET
LAKESIDE FOREST
BLOCK E

Fig. 2.—Diagrammatic profiles of four lake-side blocks at Port Victoria. The horizontal scale is much reduced.

Populations of *G. palpalis.*

In all the blocks, fly-rounds were carried out regularly on paths cut as near as possible to the edge of the water. The catching parties consisted of three fly-boys, two of whom carried between them a plain hessian screen 3 feet long by 2 feet deep. Each round was normally done once a week. The catch of non-teneral males is taken as an index of the population, and the catch of non-teneral males per 10,000 yards is conventionally called the Apparent Density. The mean monthly apparent densities in all the blocks are presented in fig. 3 (in the control block B throughout the period of 6¼ years, and in the other blocks for the shorter periods before they were interfered with by the clearing experiments). Records from an isolated block, block IX, on the Kuja river are included. Block IX was the control for the hand-catching experiment described elsewhere (Glasgow & Duffy, 1951).

TABLE III.

Trees removed from blocks C and D in the 100 feet clearing experiment (53 acres).

	Diameter in feet							
Species	½″–1½′	1½–2½′	2½–3½′	3½–4½′	4½–5½′	5½–6½′	6½–7½′	Total
Markhamia platycalyx ..	98	42	13	—	—	—	—	153
Trichilia emetica ..	46	54	20	6	1	—	—	127
Grewia sp.	77	16	—	—	—	—	—	93
Phialodiscus unijugatus ..	44	15	1	4	—	—	—	64
Ficus spp. (bongo) ..	13	26	12	4	6	—	—	61
Ficus spp. (ng'o) ..	7	25	11	4	2	7	—	56
Albizzia coriaria ..	11	19	9	10	1	—	—	50
Euphorbia candelabrum ..	34	3	4	—	—	—	—	41
Bridelia micrantha ..	10	16	6	—	—	—	—	32
Sesbania sesban	29	—	—	—	—	—	—	29
Synadenium grantii ..	23	3	—	—	—	—	—	26
Ficus spp. (pocho) ..	11	2	—	—	5	—	—	18
Acacia campylacantha ..	6	9	3	—	—	—	—	18
Kigelia aethiopica ..	—	6	—	1	—	—	—	7
Acacia sp.	3	2	1	—	—	—	—	6
Rhus sp.	4	—	—	—	—	—	—	4
Maerua sphaerocarpa ..	4	—	—	—	—	—	—	4
Euphorbia tirucalli ..	3	—	—	—	—	—	—	3
Vernonia amygdalina ..	2	—	—	—	—	—	—	2
Oncoba spinosa	1	—	1	—	—	—	—	2
Teclea nobilis	1	—	—	—	—	—	—	1
Cordia ovalis	1	—	—	—	—	—	—	1
Allophylus sp.	60	31	2	—	—	—	—	93
Acacia sp.	8	20	1	—	—	—	—	29
Sapium ellipticum ..	3	12	3	4	—	6	—	28
Pseudospondias microcarpa	9	2	1	—	—	—	—	12
Unidentified	9	—	—	—	—	—	—	9

Note: The three groups of *Ficus* spp. which are distinguished by their Luo names, are groups of species with similar habits. "Ng'o" includes *F. sycomorus*, "pocho" includes *F. thonningii*, "bongo" has large glossy leaves.

The graph shows that long-term fluctuations occur, but they are not annual and not apparently related to season. Broadly speaking, the lake-side blocks fluctuate together. The riverine block fluctuates more violently than the lake-side blocks, and the fluctuations appear to be independent of those of the lake-side blocks.

In the four lake-side blocks the density of *G. palpalis* was least in block B, followed by blocks D, E and C in ascending order. This is roughly the order of width of the habitat of *G. palpalis* shown in fig. 2, although on this basis one would have expected higher densities in block E than in block C. Perhaps a longer series of observations in block C would have shown this to be the case, as it appeared to be from September to December 1946.

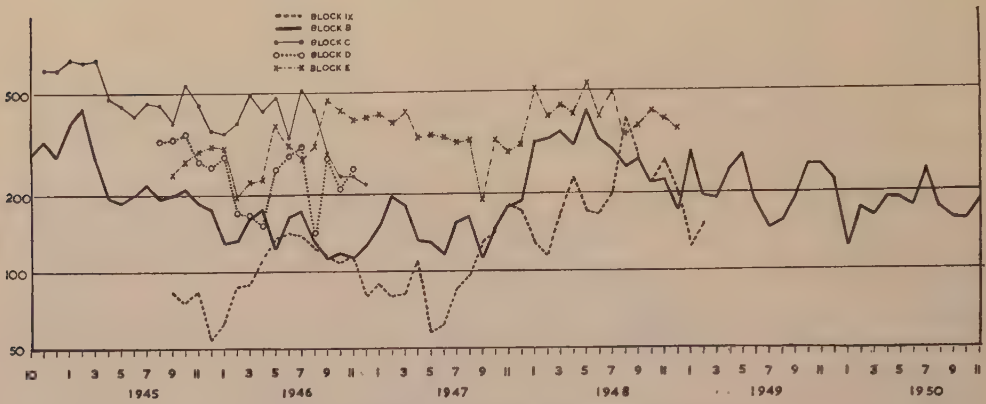


Fig. 3.—Apparent densities of *Glossina palpalis*.

Only in the case of block E has the apparent density been related to the true density. The true density, of non-teneral males only, was ascertained by releasing and recapturing marked *G. palpalis*, as detailed in Tables IX and X (pp. 572, 573). The method of calculation used is that of Jackson (1939). During the period from 22.xi.48 to 19.i.49 the mean population was 4,400, with fiducial limits 3,800 and 5,300. The mean death-rate was 26 per cent. per week, which, as the block was isolated, was a true death-rate uncomplicated by immigration or emigration. The mean length of life (the reciprocal of the death-rate) was 27 days. The undergrowth removal experiment began in half-week 16, and the first cutting was finished in half-week 29. It had been hoped that the population study would show whether this reclamation measure affected first the birth-rate or the death-rate; unfortunately the marking work was stopped too soon for this to be possible. The block was 2,200 yards long (measured along the shore) and the forest averaged about 100 yards wide, so that the area inhabited by *G. palpalis* was 45 acres. Thus the population per sq. mile was 63,000. The mean apparent density over the same period was 357 (79 per round of 2,200 yards) so that an apparent density of 1 evidently implies a population of 176 non-teneral males per sq. mile. This is a very high figure compared with what has been found for *G. morsitans* Westw. and *G. swynnertoni* Aust. With these two species an apparent density of 1 implies about 10 non-teneral males per sq. mile (Jackson, 1953). The low availability of *G. palpalis* is however confirmed by data from other places. In block VII on the Kuja river the population of non-teneral males was 1,600 in June 1946 (Glasgow, 1953). The area was 180 acres, so that this is equivalent to 5,700 per sq. mile, and since the apparent density was 65, an apparent density of 1 implied 88 non-teneral males per sq. mile. In the Sari river experiment block (Glasgow & Duffy, 1947) the population of non-teneral males was not more than 100, the area 25 acres, the apparent density 17. Here an apparent density of 1 implied 150 non-teneral males per sq. mile.

More direct evidence of the low availability of *G. palpalis* was also obtained. An observer has stood outside a thicket in sunshine and seen *G. palpalis* inside the thicket displaying no interest in him while he remained outside; when he entered the thicket they attacked him. In block D, after the lake-side forest had been removed there were for a time two fly-rounds. One was in the clearing following closely the edge of the thicket, and the other was just five yards away, inside the thicket. Both paths were less than 100 yards from the edge of the lake. The striking differences between the catches in these two situations are shown in Table IV.

TABLE IV.

Comparison between Apparent Densities of *G. palpalis* on two paths five yards apart.

	Block D	
1949	Edge of thicket	Inside thicket
January ..	36	120
February ..	23	167
March ..	21	60
April ..	26	82
May ..	22	129
June ..	18	138

The fact that *G. palpalis* is little available is thus well established by measurements in three very different situations. Casual observation, however, gives the opposite impression, for very high apparent densities of *G. palpalis* are common, and in marking experiments recaptures are easily obtained, and it is possible to get quite a high proportion of the total population marked. The anomaly is not fully understood. High apparent densities are evidently reflections of very high true densities, which are of course confined to the narrow habitats. The ease with which recaptures can be made cannot be explained. It may be that, since the distribution of *G. palpalis* is linear, it is misleading, even in a place like block E, to refer to the *area* which it is inhabiting. If this is so, it is impossible to compare the availability of *G. palpalis* directly with that of such species as *G. morsitans* and *G. swynnertoni*, whose habitats do have breadth as well as length.

Analysis of Catches of *G. palpalis* in various Situations.

Catches of lake-side *G. palpalis* made in the ordinary way, that is from a path cut close to the water's edge, contain few non-teneral females. The teneral percentage is low, and usually less than half the non-teneral males are caught on the party, the rest being caught on the ground or on vegetation. Comparable catches of riverine *G. palpalis* often have nearly as many females as males among non-tenerals, the teneral percentage is high, and more than half the non-teneral males are caught on the party. All these three criteria are considered to indicate a permanent state of relative hunger among riverine *G. palpalis*. The rule, to which no exceptions have been observed, is exemplified in Table V.

Water-borne fly-rounds were done regularly from a boat. The results from land and water rounds for eleven months in block D are compared in Table VI. The percentage of tenerals, and of non-teneral females, are higher from the boat, but the non-teneral males are fewer. Similar findings were reported by Swynnerton (1936) and by Glasgow & Duffy (1951).

Numerous observations have been made on the effect of a carried screen on catches of *G. palpalis*, but the results are still inconclusive. Between 18.ii.46 and 13.iv.46, fly-boys doing routine control of *G. palpalis* in block V on the Kuja river used hessian screens every other day. On odd days they went in parties of three with screens, and on even days in parties of two without screens. Six parties always went out, so that 18 men were used on screen days and only 12 on no-screen days. There were 24 screen days and 24 no-screen days. The results are given in Table VII. Although the numbers of tenerals and of females were higher on screen-days, this might well have been reversed had 18 men been used on no-screen days. During October to December 1946 the block C fly-round was done 21 times with a black screen, and 21 times with no screen, three fly-boys being used in each case. The procedure was to do the round with and without the screen on two successive days, starting at the same end of the round in each case. On the next pair of days the direction of the round would be reversed. The results are given in Table VIIIa, which shows that the use of the screen markedly increased the catch of tenerals and of females, though not of non-teneral males. But at the same time similar observations were made in

TABLE V.

Comparison of composition of catches of *G. palpalis* along river and lake.

	Block B at Port Victoria				Block IX Kuja river			
	Teneral %	Non-teneral females %	Non-teneral males per 10,000 yd.	Percentage of non-teneral males on party	Teneral %	Non-teneral females %	Non-teneral males per 10,000 yd.	Percentage of non-teneral males on party
1945								
September	6	1	200	33	51	41	84	61
October	12	5	209	37	37	22	76	66
November	9	4	186	46	34	27	84	62
December	14	2	173	41	44	40	54	63
1946								
January	21	5	128	63	41	40	63	67
February	13	8	131	54	51	37	87	71
March	12	4	162	52	48	37	90	87
April	13	4	174	60	40	38	111	71
May	16	0	122	57	30	37	135	72
June	12	4	162	51	34	32	142	—
July	7	2	168	40	39	28	137	70
August	15	10	133	47	29	23	122	70
September	6	2	112	52	28	25	116	66
October	8	5	118	51	25	16	107	76
November	7	2	112	32	37	17	115	73
December	16	2	125	30	47	16	80	71
1947								
January	7	3	147	39	46	20	90	63
February	7	3	196	40	39	17	80	72
March	11	2	179	34	51	28	82	82
April	7	5	133	46	47	30	110	57
May	7	3	128	37	47	41	57	55
June	3	3	116	34	48	31	62	64
July	5	4	154	36	41	11	85	—
August	6	2	164	36	36	11	95	—
September	7	3	113	35	35	24	130	—
October	6	1	149	33	30	30	142	—
November	5	1	178	34	27	26	182	—
December	6	6	187	43	28	29	168	—
1948								
January	12	8	319	39	36	32	130	—
February	8	7	322	36	26	26	115	—
March	11	4	349	31	20	29	165	—
April	9	3	307	33	28	38	230	—
May	4	2	417	28	26	39	170	—
June	6	2	321	23	28	37	167	—
July	11	2	294	28	27	25	200	—
August	4	1	249	22	28	27	392	—
September	7	4	268	33	26	23	270	—
October	9	4	221	35	33	30	217	—
November	5	2	224	27	39	29	270	—
December	16	7	169	28	38	25	200	—
1949								
January	11	9	286	40	33	40	122	—
February	7	4	194	34	24	39	152	—

block D by the same fly-boys. The arrangement was that in one week they spent four days in block C and two days in block D, then the next week they spent two days in block C and four days in block D, and so on. Only 12 pairs of observations were, however, made in block D, and the results are given in Table VIIIb. In this case the catch of females was not increased by the screen.

TABLE VI.

Comparison of composition of catches on land and in boat (block D).

	Land round				Boat round			
	Teneral %	Non-teneral females %	Apparent density	Mean catch per round, non-teneral females	Teneral %	Non-teneral females %	Apparent density	Mean catch per round, non-teneral females
1945								
December	15	4	259	3	30	44	50	10
1946								
January ..	12	8	279	6	35	42	58	11
February	10	10	169	5	26	44	47	9
March ..	8	11	167	5	17	55	35	11
April ..	10	5	135	2	25	51	26	7
May ..	8	9	253	6	7	67	30	14
June ..	7	9	280	7	19	52	33	8
July ..	7	7	306	5	18	54	62	18
August ..	12	7	141	3	20	49	34	8
September	7	5	274	4	16	45	30	7
October ..	6	5	198	3	—	—	—	—
November	3	4	249	3	16	40	24	4

TABLE VII.

Comparison of catches made by parties of 3 boys with a screen with those made by parties of 2 boys without a screen (Kuja river).

	Teneral		Non-teneral		Total		
	Males	Females	Males	Females	Males	Females	Both
Screens ..	379	331	1213	925	1592	1256	2848
No screens	336	271	1365	813	1731	1084	2815

TABLE VIII.

Comparison of catches made by parties of three, with and without screens (Berkeley Bay).

VIIIa, Block C

	Teneral		Non-teneral		Total		
	Males	Females	Males	Females	Males	Females	Both
Screens ..	36	71	2622	124	2658	195	2853
No screens	22	30	2666	63	2688	93	2781

VIIIb, Block D

Screens ..	7	26	715	23	722	49	771
No screens	12	21	711	32	723	53	776

TABLE IX.

Marking and recapture of male *Glossina palpalis* in block E, Port Victoria, from 22nd November 1948 to 23rd March 1949.

Half-week of recapture	No. caught	Half-week of release																																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
2	355	34																																		
3	343	32	28																																	
4	256	18	23	24																																
5	385	25	18	20	17																															
6	265	14	11	17	10	17																														
7	426	26	20	15	15	32	25																													
8	408	14	16	12	19	21	22	46																												
9	432	14	10	8	9	22	11	36	21																											
10	36	0	2	0	1	4	0	1	5	0																										
11	260	1	4	5	2	7	8	9	10	19	4																									
12	552	9	7	8	7	16	17	16	16	32	3	18																								
13	469	2	5	4	5	12	4	24	25	26	1	19	48																							
14	480	0	2	0	8	4	5	14	18	23	2	23	36	37																						
15	354	1	2	1	4	3	3	6	5	11	3	6	26	32	23																					
16	355	2	1	4	2	4	3	11	10	18	0	15	20	22	33	13																				
17	323	3	1	0	3	2	4	4	7	2	1	5	12	16	21	20	18																			
18	381	0	1	2	3	1	0	7	4	8	3	9	14	26	17	20	14	10																		
19	320	1			3	0	3	7	1	7		7	10	9	14	13	13	10	23																	
20	387				0	0	2	2	0	6		2	8	16	11	11	21	11	20	17																
21	411				0	2	0	1	1	5		6	8	12	12	12	15	8	20	20	22															
22	394				0	0	0	1	1	3		1	3	10	10	12	9	8	13	20	19	21														
23	339				1	3	1	4		1		0	5	6	2	4	8	10	9	13	13	20	14													
24	169					0	0	0				2	1	2	1	4	2	5	5	6	6	11	7	8												
25	278					0	1	1				1	1	5	2	4	5	4	4	5	6	21	11	14	8											
26	293					0	1	0				0	1		4	4	2	6	5	5	3	8	7	18	10	15										
27	196					0		0				0	1		0	1	1	1	2	3	5	2	5	10	3	8	8									
28	165					1		1				0			1	3	1	0	2	3	3	2	6	6	4	7	8	4								
29	292					1						0			0		0	0	3	5	3	3	11	5	6	11	9	16	9							
30	105											0			1		1	0		1	1	0	2	3	3	3	1	2	5	7						
31	120											0			0			0		0	2	0	1	1	2	3	2	3	4	4	5					
32	140											1			1			0		1		0	1	4	2	4	8	0	0	6	3	11				
33	72																	0				0		1		1	1	5	2	2	3	2	4			
34	87																	1				0		2		0	1	3		2	2	2	2	1		
35	127																					1				1		1		3	2	5	2	3	3	
No. released		437	370	357	271	408	277	447	429	450	41	271	568	524	525	391	365	343	391	335	401	432	413	351	181	295	307	221	170	302	108	129	147	83	93	

Note : This Table is a " Fisher lattice." These are usually presented as right-angled isosceles triangles with the hypotenuse at the top and the right angle at the bottom centre. This one has been swung through 45°, thus making the NW-SE lines into columns and the NE-SW lines into rows ; like this it is much easier to type and print. It is compiled by the " double-entry " method (Method A of Leslie & Chitty, 1951). That is to say, a fly recaptured more than once is entered each time as a recapture against every previous date on which it was released, not only against the last date (Method B) nor only against the first date (Method C).

TABLE X.

Corrected recaptures of male *Glossina palpalis*.

Half-week of release

Half-week of recapture	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
2	2·19																																	
3	2·13	2·21																																
4	1·61	2·43	2·63																															
5	1·49	1·26	1·46	1·63																														
6	1·21	1·12	1·80	1·39	1·57																													
7	1·40	1·27	0·99	1·30	1·84	2·12																												
8	0·79	1·06	0·82	1·72	1·26	1·95	2·52																											
9	0·74	0·63	0·52	0·77	1·25	0·92	1·86	1·13																										
10	0·00	1·50	0·00	1·03	2·72	0·00	0·62	3·24	0·00																									
11	0·09	0·42	0·54	0·28	0·66	1·11	0·77	0·90	1·62	3·75																								
12	0·37	0·34	0·41	0·47	0·71	1·11	0·65	0·68	1·29	1·33	1·20																							
13	0·10	0·29	0·24	0·39	0·63	0·31	1·14	1·24	1·23	0·52	1·49	1·80																						
14	0·00	0·11	0·00	0·62	0·20	0·38	0·65	0·87	1·06	1·02	1·77	1·32	1·47																					
15	0·06	0·15	0·08	0·42	0·21	0·31	0·38	0·33	0·69	2·07	0·63	1·29	1·73	1·24																				
16	0·13	0·08	0·32	0·21	0·28	0·31	0·69	0·66	1·13	0·00	1·56	0·99	1·18	1·77	0·94																			
17	0·21	0·08	0·00	0·34	0·15	0·45	0·28	0·51	0·14	0·76	0·57	0·65	0·95	1·24	1·58	1·53																		
18	0·00	0·07	0·15	0·29	0·06	0·00	0·41	0·24	0·47	1·92	0·87	0·65	1·30	0·85	1·34	1·01	0·77																	
19	0·07			0·35	0·00	0·34	0·49	0·07	0·49		0·81	0·55	0·54	0·83	1·04	1·11	0·91	1·84																
20				0·00	0·00	0·19	0·12	0·00	0·34		0·19	0·36	0·79	0·54	0·73	1·49	0·83	1·32	1·31															
21				0·00	0·12	0·00	0·05	0·06	0·27		0·54	0·34	0·56	0·56	0·75	1·00	0·57	1·24	1·45	1·33														
22				0·00	0·00	0·00	0·06	0·06	0·17		0·09	0·13	0·48	0·48	0·78	0·63	0·59	0·84	1·52	1·20	1·23													
23				0·11	0·22	0·11	0·26		0·07		0·00	0·26	0·34	0·11	0·30	0·65	0·95	0·60	1·14	0·96	0·37	1·00												
24					0·00	0·00	0·00				0·44	0·10	0·23	0·11	0·61	0·32	0·86	0·76	1·06	0·89	1·51	1·00	1·35											
25					0·00	0·13	0·08				0·13	0·06	0·34	0·14	0·37	0·49	0·42	0·37	0·54	0·54	1·75	0·96	1·43	1·59										
26					0·00	0·12	0·00				0·00	0·06		0·26	0·35	0·19	0·60	0·44	0·51	0·26	0·63	0·58	1·75	1·89	1·74									
27					0·00		0·00				0·00	0·09		0·00	0·13	0·14	0·15	0·26	0·46	0·64	0·24	0·62	1·45	0·85	1·38	1·33								
28					0·15		0·14				0·00			0·12	0·47	0·17	0·00	0·31	0·54	0·45	0·28	0·88	1·04	1·34	1·44	1·58	1·10							
29					0·08						0·00			0·00		0·00	0·00	0·26	0·51	0·26	0·24	0·91	0·49	1·14	1·28	1·00	2·48	1·81						
30											0·00			0·18		0·26	0·00		0·28	0·24	0·00	0·46	0·82	1·58	0·97	0·31	0·86	2·80	2·21					
31											0·00			0·00			0·00		0·00	0·42	0·00	0·20	0·24	0·92	0·85	0·54	1·13	1·96	1·10	3·86				
32											0·26			0·14			0·00		0·21		0·00	0·17	0·81	0·79	0·97	1·86	0·00	0·00	1·42	1·98	6·09			
33																	0·00				0·00		0·40		0·47	0·45	3·14	1·63	0·92	3·86	2·15	3·78		
34																	0·34				0·00		0·65		0·00	0·37	1·56		0·76	2·13	1·78	1·56	1·38	
35																					0·18				0·27		0·36		0·78	1·46	3·05	1·07	2·85	2·54

Note: These corrected recaptures are the values expected if releases and recaptures in each half-week had been exactly 100. Thus, in half-week 3, the corrected recapture of flies marked in half-week 2 was 2·21. This is calculated from the actual recapture, 28, by dividing by 370, the number released in half-week 2, and by 343, the number caught in half-week 3, and then multiplying by 100^2.

Summary.

Glossina palpalis fuscipes Newst. was studied in lake-side forest in north-east Lake Victoria and in riverine forest on the Kuja river, which runs into Lake Victoria. Climatic records are given. Tree counts were made in fifty acres of lake-side forest.

Populations of *G. palpalis* exhibit long-term fluctuations which are not annual and not related to season. On the lake shore, the density of *G. palpalis* is roughly correlated with the width of the forest, being least where the forest is narrow. In a block 2,200 yards along the shore by 100 yards wide (this was the widest forest studied) the population was 4,600 non-teneral males. The mean catch along the 2,200 yards of shore was 78 non-teneral males. Calculated on an area basis, this is more than ten times the population which would be inferred from the same catch of *G. morsitans* or *G. swynnertoni*. The mean death-rate in this isolated block was 26 per cent. per week, and the mean length of life was 27 days.

Analysis of catches indicates that riverine *G. palpalis* are always more hungry than those on the lake shore, for the percentages of tenerals, of females, and of males attacking, are all higher on the river. Catches from a boat produce more females but fewer males than land catches. Carrying a screen produced more females on some occasions, but not on others, the discrepancy being unexplained.

Acknowledgements.

Messrs. F. Wilson and A. N. Smit were successively in charge of the Port Victoria station and collected most of the data considered here.

References.

Glasgow, J. P. (1953). The extermination of animal populations by artificial predation and the estimation of populations.—J. Anim. Ecol., **22,** pp. 32–46.

Glasgow, J. P. & Duffy, B. J. (1947). The extermination of *Glossina palpalis fuscipes*, Newstead, by hand-catching.—Bull. ent. Res., **38,** pp. 465–477.

Glasgow, J. P. & Duffy, B. J. (1951). Further observations on the extermination of *Glossina palpalis fuscipes*, Newstead, by hand-catching.—Bull. ent. Res., **42,** pp. 55–63.

Jackson, C. H. N. (1939). The analysis of an animal population.—J. Anim. Ecol., **8,** pp. 238–246.

Jackson, C. H. N. (1953). A mixed population of *Glossina morsitans* and *G. swynnertoni*.—J. Anim. Ecol., **22,** pp. 78–86.

Leslie, P. H. & Chitty, D. (1951). The estimation of population parameters from data obtained by means of the capture-recapture method.—Biometrika, **38,** pp. 269–292.

Swynnerton, C. F. M. (1936). The tsetse flies of East Africa.—Trans. R. ent. Soc. Lond., **84,** pp. 1–579.

Symes, C. B. & Southby, R. (1938). The reduction of *G. palpalis* in a lake shore area by the " block " method.—32 pp., Nairobi, Govt. Printer.

AN INVESTIGATION OF THE DISTRIBUTION AND FIELD HABITS OF THE VARIED CARPET BEETLE, *ANTHRENUS VERBASCI* (L.) (COL., DERMESTIDAE) IN BRITAIN, WITH COMPARATIVE NOTES ON *A. FUSCUS* OL. AND *A. MUSEORUM* (L.).

By G. E. Woodroffe and B. J. Southgate.
Department of Scientific and Industrial Research,
Pest Infestation Laboratory, Slough, Bucks.

(Plates XXXVIII–XL.)

This work was undertaken as a supplement to a laboratory study of the life-history and behaviour of *Anthrenus verbasci* (L.) which is being carried out by Mrs. G. M. Blake of the Pest Infestation Laboratory. Its purpose was to provide information upon which control measures might be based. Throughout this investigation attention was paid to the two other common species of *Anthrenus*—*A. fuscus* Ol. and *A. museorum* (L.)—and a comparison was made between these species and *A. verbasci*.

Two factors are of obvious importance when considering distribution—the natural geographic range of the species, determined by climatic factors, and the locality distribution, determined by the occurrence of the preferred habitat. Three survey methods were used to study these points—the collection of adults from flowers during May, June and July; the collection of larvae from natural habitats (certain birds' nests, under the bark of trees, etc., *cf.* Woodroffe, 1953); and the inspection of infested premises. These investigations also yielded a considerable amount of information on the field habits of the three species concerned.

Collection of Adults from Flowers.

Adults of *Anthrenus* appear in the open at the end of May and may be found on flowers until early August. The numbers usually reach a peak during June, the precise date depending upon the weather. Indoors, especially in heated buildings, adults may be found upon the windows from March onwards. The beetles are attracted to certain flowers where they feed upon nectar and pollen and where copulation may frequently be observed. The most attractive plant, and that most commonly used for collection of beetles, was found to be hogweed, *Heracleum sphondylium*. Other plants used, and important when hogweed was absent, were wild chervil (*Anthriscus sylvestris*), goutweed (*Aegopodium podagraria*), yarrow (*Achillea millefolium*), wild carrot (*Daucus carota*), chamomile and mayweed (*Matricaria* spp. and *Anthemis* spp.).

During the summers of 1951 and 1952, adults of *Anthrenus* were collected in a number of widely separated localities in England and the proportions of the three species in each collection determined. The composition of the population of *Anthrenus* in the grounds of the laboratory was used as a standard for comparison with collections made elsewhere. This was necessary because preliminary observations indicated that adults of *A. verbasci* appeared in numbers in the open rather earlier in the year than those of *A. fuscus* or *A. museorum*. Thus the absence of a species from any locality was considered significant only if that species was present in the control population at that time.

Altogether 200 individual collections were made, and this figure includes those occasions when suitable plants yielded no beetles. The total of 5,300 adults identified comprised 3,020 *A. verbasci*, 2,240 *A. fuscus* and 40 *A. museorum*. These figures cover only the field trips and do not include the several thousand adults collected in the laboratory grounds, where, over a complete season (late May to early August) the proportions of the three species were of the order 10 *A. verbasci*: 4 *A. fuscus*: 1 *A. museorum*. Mixed populations of this kind were seldom encountered on the field trips. If a species occurred in large numbers at any locality it was usually accompanied by, at most, only a few individuals of the other two species. The reasons for this will be discussed later.

The results of the flower-head survey may be summarised as follows:—

A. verbasci.

Geographic range.—Joy (1932) gives the range of this species in Britain as England and S.E. Scotland. In contrast to this, we failed to capture a single specimen of *A. verbasci* on flowers north of the line Bedford–Gloucester. If, therefore, they occur at all in the north, the numbers must be extremely small. The abundance of the species also falls off rapidly west of the line Bedford–Southampton.

Locality preference.—*A. verbasci* was found to be an inhabitant of suburban areas. It was never found further from buildings than about 100 yards and was largely confined to the belt of residential suburb which surrounds the larger towns. It was generally absent from the older built-up areas and city centres although, on one occasion, 150 *A. verbasci* and 2 *A. fuscus* were swept from a small patch of goutweed in the centre of Canterbury. It was absent, also, from farms, villages and small country towns except in S. Essex and N. Kent where scattered urban development had enabled it to become more generally distributed.

A. fuscus.

Geographic range.—Joy (1932) gives England from the south to Yorkshire as the range of this species in Britain. This is probably accurate although we found that the numbers present in the north were small. It extended to the west in undiminished numbers.

Locality preference.—*A. fuscus* was distributed very much more generally than *A. verbasci*. A few adults were collected in central London but the species occurred most abundantly in rural areas, where it was found far removed from buildings. It was seldom as plentiful as *A. verbasci* in suburban areas except in the vicinity of sheds and outbuildings. A noteworthy exception was the capture, in a locality typical of *A. verbasci* in the eastern outskirts of Swindon, of 2 *A. verbasci* and 126 *A. fuscus*.

A. museorum.

This species was found only in small numbers, so no definite conclusions concerning its distribution could be reached, but it appeared to resemble *A. fuscus* rather than *A. verbasci*. Joy (1932) includes all England within its range. It appeared to be confined to the vicinity of buildings to a greater extent than *A. fuscus*.

Collection of Larvae from Natural Habitats.

The most important natural habitat of *A. verbasci* in Britain is the dry birds' nest (*vide* Woodroffe & Southgate, 1951; Woodroffe, 1953). Such nests are usually confined to buildings and thus nests of the house-sparrow (*Passer domesticus*), house-martin (*Delichon urbica*), swallow (*Hirundo rustica*), jackdaw (*Corvus monedula*), starling (*Sturnus vulgaris*), swift (*Apus apus*) and city pigeon (*Columba* sp.) are of greatest importance. During the nest survey, *A. verbasci* was recorded from about 60 per cent. of all sparrow, martin and swallow nests examined. The distribution of *A. verbasci* revealed by these nest records corresponded closely with that deduced from the collection of adults from flowers.

While *A. verbasci* is characteristically an inhabitant of dry birds' nests, *A. fuscus* is found most commonly in the nests of social insects, under the bark of trees, around spiders' webs (Pl. XXXVIII) in outhouses and in crevices in fences. In connection with the last-mentioned habitat it is worth recording that when the weatherboard boundary fence of the laboratory was replaced, ten sections were carefully examined and 150 larvae of *Anthrenus* were collected from the crevices. When reared, two proved to be *A. verbasci* and the remainder *A. fuscus*. The abundance of habitats suitable for *A. fuscus* in the laboratory grounds doubtless explains the rather high proportion of this species in the control population as compared with most collections made in areas where *A. verbasci* was normally dominant. On only two occasions was *A. fuscus* found in the *A. verbasci* type of habitat and in each case a sparrows' nest in a farm barn had been utilised. There was, however, an abundance of old spiders' webs and dead insects in the immediate vicinity of these nests, so they may have been accidentally colonised by larvae rather than selected as oviposition sites by the adults.

Little information was obtained concerning the larval habitat of *A. museorum*. It was presumed to be similar to that of *A. fuscus* for occasional individuals were discovered among collections of *A. fuscus* larvae. One birds' nest from Carlisle contained some cast larval skins and examination of the few remaining sagittal hairs indicated that the larvae had been *A. museorum* (Hinton, 1945). In the laboratory grounds, adults of *A. museorum* were not uncommon but were distributed rather more locally than either of the other species. They occurred annually in some numbers in, on or near one or two particular outbuildings, but only rarely elsewhere. Unfortunately it was not possible to discover where the larvae were feeding, but rodents' nests, or dead rodents, beneath the floorboards seemed the most likely possibility.

Inspection of Infested Premises.

In response to a number of articles in the press many enquiries were received from members of the public who had discovered larvae of *Anthrenus* damaging household materials and clothing. On about 50 occasions an inspection of the premises was carried out and much information on the field habits of the larvae has been obtained. It was noteworthy that most of the enquiries came from the suburban fringe of the Greater London area, and these usually from districts which, from the collections of adults made during the summer, were known to be heavily infested. A few complaints were received from the larger coastal towns in the south-west which again confirmed our earlier conclusions. No enquiries came from Bristol where, rather surprisingly, very few adults were collected in the summer. Several samples of larvae were received from northern areas but all were *A. fuscus*. Once two adults of *A. verbasci* were received from a householder who found them indoors at Birkenhead.

The general pattern of the domestic infestation.

The majority of household infestations were found to conform to a single general pattern. In almost every case the householder complained of damage at first in the airing-cupboard and subsequently in other, or all, upstairs rooms. Often no larvae had been noticed downstairs, or, if present, the numbers were small. Inspection revealed that the attic or roof-space was usually an important source of larvae. Birds' nests in the attic were often heavily infested—on one occasion 363 larvae were separated from a single sparrows' nest. Dead birds were sometimes important—in one instance two dead sparrows from an infested attic yielded 69 larvae (Pl. XXXIX). Frequently a variety of old woollen garments or bedding had been used to protect the water-tank and pipes from frost and these were often reduced almost to powder by the activities of the larvae. Once 88 larvae were obtained from the lagging on 3–4 feet of water-pipe. A wide variety of other articles, and much of the rubbish so frequently stored in attics, was found to support a variable number of larvae.

The migration of larvae—mostly fully grown—from the attic to the inhabited rooms of the house took place largely in the autumn (September–October) although migration on a small scale probably occurred at other times. The importance of the airing-cupboard as the apparent source of the infestation in most cases suggested that the aperture through which the water-pipes passed from the attic tank into the airing-cupboard to supply the hot tank was an important route for migrating larvae. This was an obvious route for larvae infesting lagging on these pipes. That such migration does, in fact, take place has not been conclusively proved, but the evidence in its favour is very strong. On more than one occasion a householder described how the airing-cupboard and all its contained clothing was carefully cleaned and disinfested following discovery of larvae, but, on replacing the clothing, reinfestation occurred overnight. Movement of larvae from attic to house was frequently possible by way of the trap-door, which seldom fitted tightly enough to hinder the passage of small insects. Occasionally various other holes seemed to have been used.

Spread of wandering larvae round the house was largely by way of cavity walls and air-bricks, skirting boards, picture rails, floor cracks, etc., and was probably facilitated on some occasions by transfer of infested clothing from the airing-cupboard to the bedrooms. Adults produced by these larvae would then be found on the windows of the various rooms in spring and early summer.

Factors affecting the degree of infestation.

The importance of birds' nests, especially house-sparrows' nests, in initiating the more severe infestations has been fairly conclusively demonstrated. In the absence of such nests, and provided the house was situated in a heavily infested area, the adults, which were abundant outside during June and July, entered the house in a variety of ways and gave rise to a diffuse infestation. In such cases the larvae were found distributed throughout the house in small numbers and some doubtless originated from eggs laid in floor cracks, under skirting boards and similar undisturbed crevices. In the attic, when there was no obvious and ample food supply, the larvae were found distributed over the floor and on the rafters, where they apparently fed upon dead insects and other small fragments of organic débris. The incidence of the diffuse type of infestation was probably controlled to some extent by the distribution of those flowers which are most attractive to the adults. Such flowers often produce very dense local aggregations of adults—on occasions 100 or more adults of *A. verbasci* may be counted on a single head of hogweed—and, if situated close to a particular house, may considerably increase the probability of a diffuse infestation by more or less random entry of adults.

The amount of damage sustained in the inhabited rooms of a house was not entirely dependent upon the density of the attic population. The absence of a roof tank supplying water to a hot tank in an airing-cupboard, combined with a tight-fitting trap-door, could render the inhabited rooms of the house almost inaccessible to migrating larvae, and, in some instances, this was thought to have been the case. Conversely, a diffuse attic infestation occasionally caused significant damage because of the ease with which the larvae could invade the house. In one case ventilation grids opening from the attic into built-in wardrobes in two bedrooms enabled a very diffuse attic infestation to cause a relatively large amount of damage.

The possibility that adults might enter a house through an open window and deposit eggs beneath skirting boards, etc., or directly upon clothing or under carpets has already been mentioned, but on no occasion were young larvae or their cast skins discovered in such situations. There were, however, other places where, in isolated instances, breeding occurred. Disused or boarded-up chimneys, possibly containing nests, sometimes proved to be a source of larvae. Occasionally a disused cupboard or the space beneath a panelled bath supplied evidence that a few larvae had grown to maturity there. But, in all such cases, the numbers of larvae were quite insignificant compared with those normally found in the roof-space.

Infestation of commercial premises.

No example has yet been brought to our notice of large-scale damage to commercial stocks of woollen materials by *A. verbasci*. The only instances affecting textile trades concerned small retailers of woollen goods. All cases of damage in this category have been followed up by an inspection of the premises. In no case was the damage severe, but the loss of goodwill resulting from the sale of damaged garments caused the retailers some concern. All the infestations were of the diffuse type, originating in some dirty, undisturbed recess of the type already described.

Unusual damage occurred in a telephone exchange in Kent, where electrical faults in 7 out of 25 manually operated switchboards on the top floor were traced to damage by larvae of *A. verbasci* and the common clothes moth, *Tineola bisselliella* (Humm.). The insects were feeding upon the insulation—a wool-cotton mixture—of certain wires which were bound into " forms ", *i.e.*, thick ropes of wires, an inch or more in diameter (Pl. XL). The source of the *Anthrenus* appeared to be a number of sparrows' nests in an adjoining building, the eaves of which were on a level with, and very close to, the windows of the exchange. These windows were open day and night throughout the summer.

Discussion.

In view of its limited objective, this work was not expected to produce results which allowed any far-reaching conclusions to be drawn. It has, however, supplied a certain amount of information likely to be of value to those concerned with the control of carpet beetles and has also indicated several lines along which biological investigations might profitably be directed.

Distribution.

When an insect—particularly a pest species—becomes well-known and widely recognised, it is inevitable that it should, at the same time, appear to become more abundant. However, we do not consider that this fact can, by itself, explain the spectacular increase in the incidence of damage by carpet beetles which has apparently taken place in south-east England during the last ten years. If, as seems likely, a considerable actual increase has occurred, it is explainable in four ways.

Importation.—The present distribution of *Anthrenus verbasci*, considered in the light of its recent rapid increase, strongly suggests that the species is a recent importation. However, records of its occurrence in this country go back 100 years or more. For example, Hinton (1945) quotes Parfitt (1867) for a record from flowers in Britain, so the importation hypothesis can apply only to the possible importation of a different strain of the same species. This would be difficult to prove or disprove.

Climatic change.—It is possible that some slight change in the climate of south-east England has occurred comparatively recently and that this has enabled the observed increase to take place. Against this, there is, so far, no evidence from life-history studies (Blake, unpublished) that any particular combination of physical conditions likely to have resulted from a small climatic change is of critical importance for the insect's development or survival. In view of the protection from climatic conditions experienced by larvae which develop indoors, it seems probable that any slight change would first affect the adults, because of their occurrence in the open. If this is so, then summer conditions are the most important. It is interesting that a considerable number of insects appear to have increased their numbers or extended their ranges at about the same time as *A. verbasci.* Unfortunately, unless the insect is large or, for some other reason, is unlikely to have been overlooked, there remains always a doubt concerning its former status and the familiar argument quoted at the beginning of this discussion of distribution casts doubt upon the reality of the increase. There is, however, at least one good example concerning which there can be little doubt. Up to 1943, less than a dozen British specimens of the large and conspicuous Syrphid, *Volucella zonaria* (Poda) were known, and several of these were only doubtfully British (Goffe, 1945). The species is now widely distributed in at least the southern half of the country. This increase must have occurred concurrently with that of *A. verbasci.*

Spread of suburban areas.—The marked preference of *A. verbasci* for suburban areas suggests that the rapid spread of such development during the last 30 years may have had an important effect upon the abundance of this pest. From what has already been said it is obvious that many modern improvements in house construction—*e.g.*, cavity walls, hot-water systems, etc.—have been to the advantage of the beetle as well as the human occupants. Certain other features of modern building which must be placed on the debit side of the human account—*e.g.*, unseasoned wood, inferior quality plaster carelessly applied, etc.—are also beneficial to the insect. Also, the suburban housing estate, with its considerable sparrow population, and its vacant plots and odd corners of waste land upon which hogweed and other attractive plants grow freely, is eminently suitable for the rapid spread of this species. This does not, however, explain its surprising absence from such places as Birmingham and Bristol unless some climatic factor is also operative or unless the insect responds only slowly to the changed conditions, and the increase in areas other than the south-east is yet to come.

It is noteworthy that neither *A. fuscus* nor *A. museorum* appear to have increased to any remarkable extent. There may be important differences between these species and *A. verbasci* for, even under favourable conditions, they do not appear to be capable of becoming serious pests. One case of damage by *A. fuscus* was thoroughly investigated. It occurred in one wing of a large country house which had not been cleaned since its war-time occupation by military personnel seven years previously. Although proof was obtained of direct attack by ovipositing adults upon carpets, the amount of damage throughout the wing was remarkably small.

Change of habits or behaviour of the insect.—The possibility that a strain of *A. verbasci*, more closely adapted to conditions in suburban areas than the native stock, may have been recently imported has already been mentioned. It is equally possible that such a strain has arisen locally and is now spreading across the country in suitable areas. It is very unlikely that this can be proved and an argument against it, as against the idea of importation, is that the new strain would have been rapidly distributed to all the major population centres by transport of infested articles, and these areas would now show large populations of *Anthrenus verbasci.* That this has not occurred can be satisfactorily explained only by postulating a favourable climatic change in the south-east which has not occurred elsewhere.

Habitat preference.

The differences in larval habitat between *A. verbasci* and *A. fuscus* are reflected in their observed locality distribution. Habitats suitable for *A. fuscus* are plentiful in open country and probably reach a peak in the vicinity of farms. If, however, the habitat preference is sharply defined, as in *A. verbasci*, areas of open country, even if of comparatively small extent, will prove barriers which *A. verbasci* will cross only with difficulty, as dry birds' nests—the typical habitat of this species—are scarce in such areas. One example already quoted (larvae collected from fence—see p. 577) illustrates that *A. verbasci* only very rarely invades the *A. fuscus* type of habitat. The damage by *A. fuscus* in the country house already referred to indicates that isolated habitats suitable for *A. verbasci* (the house contained many nests) are seldom actually occupied by that species. Two other examples are worthy of mention. At Rothamsted Experimental Station, Harpenden, Herts., the upper floor of an old coach-house was colonised by jackdaws. Nests were removed and examined, but no *Anthrenus* larvae were found. Larvae of *A. fuscus* were, however, abundant round the windows, feeding upon the remains of dead insects. On an Essex farm, collection of adults from flowers revealed the presence of a very large *A. fuscus* population. Thousands of adults were flying round a *Spiraea* bush which was situated close to the entrance of a hornets' nest (*Vespa crabro* L.) in the farmhouse. However, when sparrows' nests were removed from the stables and cart-sheds later in the year they contained only a few larvae of *A. verbasci* and none of *A. fuscus*. Both these examples illustrate that *A. fuscus* does not normally utilise the habitat preferred by *A. verbasci*.

Both species can develop satisfactorily in nests and on dead insects, so it seems likely that each possesses an adult behaviour reaction which ensures that eggs are usually laid in appropriate situations.

Household infestations.

The importance of *A. verbasci* as a household pest in the suburban areas of south-east England was clearly demonstrated by the spate of enquiries which followed the appearance of articles in the national press. In these areas it is probably more important than the common clothes moth. There are several reasons for this. Firstly, while the damage caused by larvae of *A. verbasci* is seldom extensive, new or clean materials are frequently attacked. This is because the larvae are already nearly full-grown when they migrate from the attic to the house and thus no longer require certain essential food factors in which clean wool is notably deficient. Secondly, ordinary household hygiene, which can control the common clothes moth, is ineffective against carpet beetle because of the migratory habits of the larvae. Thirdly, in a heavily infested area, the efforts of one household to control the pest will be fruitless unless supported by similar action in neighbouring houses. Unless the overall population of such an area is reduced, repeated infestations of the diffuse type are certain to occur. Fourthly, the insect is very resistant to all the usual insecticides (Dr. E. A. Parkin, of the Pest Infestation Laboratory, unpublished).

During this survey certain biological problems appeared to be of considerable importance in elucidating the precise mechanism of the household infestation, and these are briefly stated below.

1. The behaviour reactions which guide the adult from the flower-head to the attic. The reasons for the choice of the attic as the main oviposition site and the importance of birds' nests in guiding this selection.
2. The influence of nest conditions, especially temperature, on larval development.
3. The mechanism of larval migration—*i.e.*, the stimuli which initiate it and guide the wandering larvae into the inhabited rooms; the precise routes taken

and the distances travelled by the migrating larvae; and the proportion of the attic population which take part in the autumnal migration.

4. The nature of the damage. Whether the wandering larvae are feeding, or casually boring holes in various materials for reasons not connected with food requirements.

5. The relative importance of the attic as compared with other suitable sites, as a source of larvae, particularly in diffuse infestations.

6. The extent to which mating and oviposition occur in the original breeding site before the adults leave the house and, following from this, the importance of the flower-head aggregations in providing opportunities for repeated mating, thus possibly stimulating oviposition.

Some of these problems are the subject of current experimental studies by Mrs. G. M. Blake, of the Pest Infestation Laboratory.

Summary.

Conclusions concerning the distribution and field habits of *Anthrenus verbasci* (L.), *A. fuscus* Ol. and *A. museorum* (L.) are based upon the results of three surveys.

The first survey comprised the collection of adults of *Anthrenus* from attractive flowers, *e.g.*, hogweed, *Heracleum sphondylium*, in various localities during June and July. This showed that:—

A. verbasci occurred in large numbers only in the suburban areas of south-east England, extending also to the west along the south coast.

A. fuscus was generally distributed in all types of locality in the south, reaching a peak abundance in the vicinity of farms. Its numbers diminished rapidly towards the north.

A. museorum occurred in small numbers only, often accompanying *A. fuscus*.

The second survey comprised the collection of larvae from natural habitats and included results from an earlier survey of certain birds' nests. This showed that:—

A. verbasci was characteristically an inhabitant of dry birds' nests.

A. fuscus was usually found feeding on dead insects around spiders' webs, under the bark of trees, etc.

A. museorum occurred in small numbers in company with *A. fuscus*.

The habitat difference between *A. verbasci* and *A. fuscus* was sharply defined. Only very rarely was one species found in the habitat typical of the other.

The third survey comprised the inspection of infested premises. This confirmed the distribution results provided by the other two surveys and provided information concerning the habits of *A. verbasci* in infested premises, which included the following main points:—

Infestations in private houses were generally divisible into two types: heavy infestations, in which birds' nests in the attic usually played an important part, and diffuse infestations, in which nests were absent, and very much smaller numbers of larvae were concerned. In both types the attic appeared to be the chief source of larvae and infestation of lagging on water-pipes was often a conspicuous feature. In the diffuse type other sources of larvae were probably of some importance.

Damage was caused mainly by larvae that wandered from the attic in the autumn. The most usual migration route was via the water-pipes which passed from the attic tank to the airing-cupboard, or by way of the trap-door opening into the attic, although other routes were sometimes used. Larvae which developed elsewhere, *e.g.*, in cavity walls or behind skirting boards, seemed to wander at about the same time.

New or clean clothing was frequently damaged by the wandering larvae.

Damage to stock in commercial premises was sometimes sustained by small retailers of woollen goods. Such infestations were always of the diffuse type.

In one instance electrical faults in a telephone exchange were found to be due to damage caused by larvae of *Anthrenus verbasci* to the insulation of certain wires.

In discussion of these results possible reasons for the recent increase and present distribution of *A. verbasci* are considered. Possibilities mentioned are importation, climatic change, spread of suburban areas and change of habits or behaviour of the species. The observed locality distribution of the three species is correlated with their preferred larval habitats.

Some biological problems with particular bearing upon the household infestation are listed.

Acknowledgements.

Plates XXXVIII and XXXIX were taken by Mr. J. H. Hammond, of this Laboratory. Plate XL was taken by Mr. L. G. Ramell, of Canterbury, and we are indebted to him for permission to reproduce it.

This work forms part of the research programme of the Pest Infestation Laboratory, and is published by permission of the Department of Scientific and Industrial Research.

References.

Goffe, E. R. (1945). *Volucella zonaria* (Poda, 1761) (Dipt. Syrphidae) in Britain.—Ent. mon. Mag., **81**, pp. 159–162.

Hinton, H. E. (1945). A monograph of the beetles associated with stored products. I.—443 pp. London, Brit. Mus. (Nat. Hist.).

Joy, N. H. (1932). A practical handbook of British beetles.—622 pp. London, Witherby.

Woodroffe, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain.—Bull. ent. Res., **44**, pp. 739–772.

Woodroffe, G. E. & Southgate, B. J. (1951). Birds' nests as a source of domestic pests.—Proc. zool. Soc., Lond., **121**, pp. 55–62.

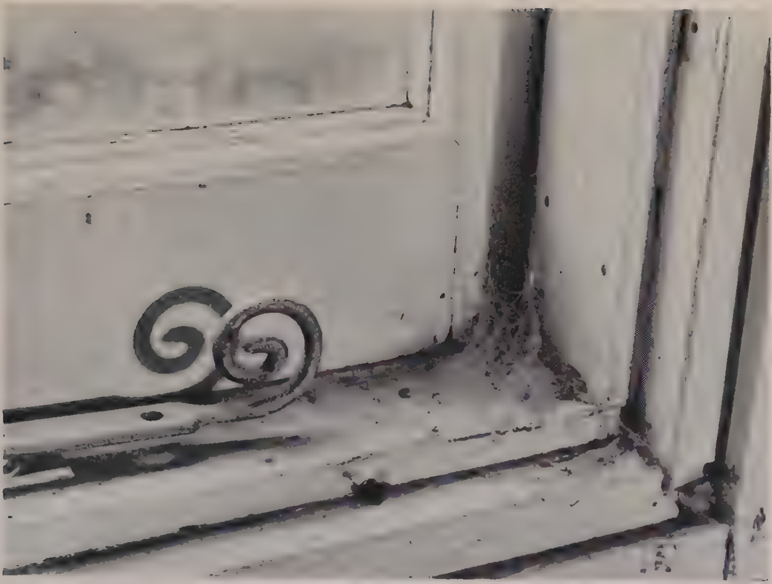


FIG. 1. Spiders' webs and dead insects on a window ledge.

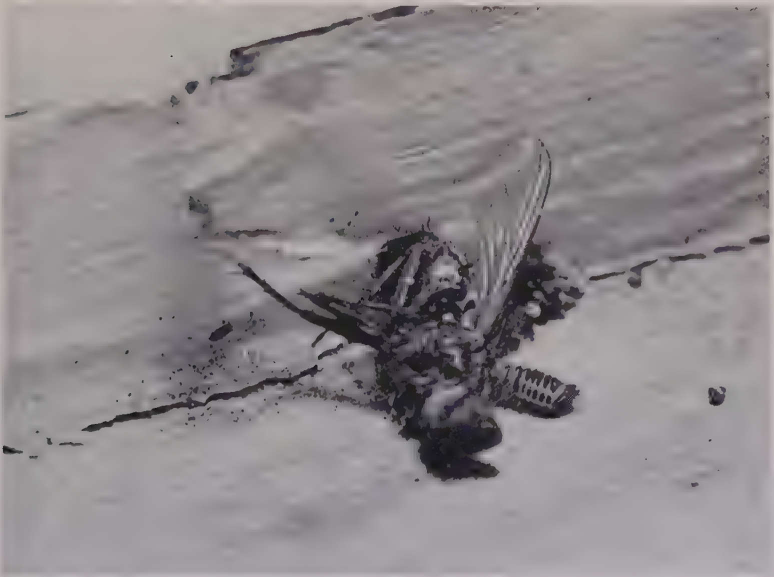


FIG. 2. Larva feeding on dead blow-fly.

TYPICAL LARVAL HABITAT OF *ANTHRENUS FUSCUS*.

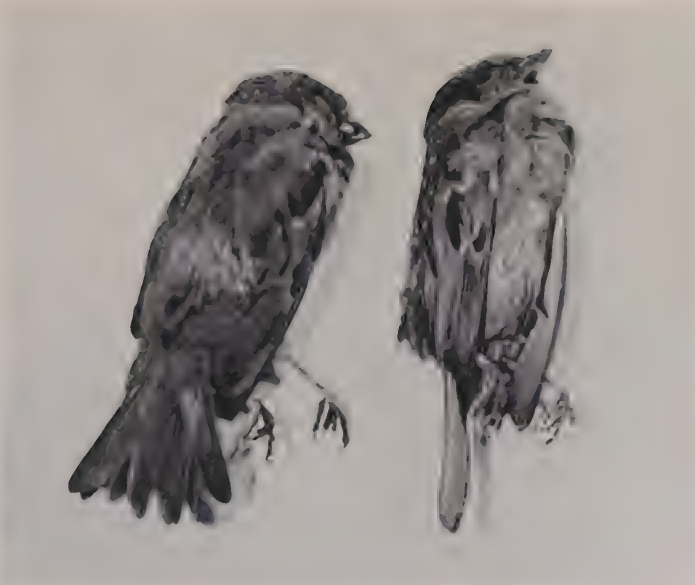


FIG 1. Dead sparrows from an infested attic.

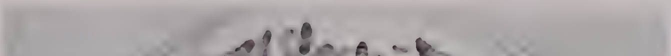
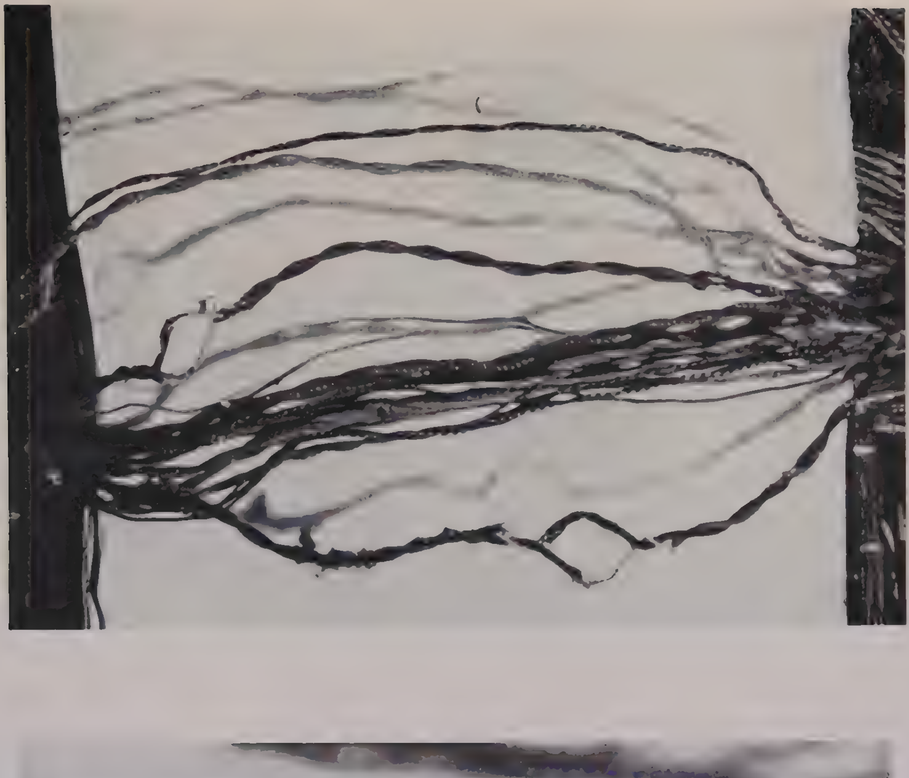


FIG. 2. Larvae extracted from dead sparrows.

A LARVAL HABITAT OF *ANTHRENUS VERBASCI.*



Unusual damage by larvae of *Anthrenus verbasci;* destruction of insulation on wiring in a telephone exchange.

AIRCRAFT APPLICATIONS OF INSECTICIDES IN EAST AFRICA. VI.—APPLICATIONS OF A COARSE AEROSOL CONTAINING DDT TO CONTROL THE TSETSE FLIES, *GLOSSINA MORSITANS* WESTW., *GLOSSINA SWYNNERTONI* AUST. AND *GLOSSINA PALLIDIPES* AUST.

L. G.

By K. S. Hocking, D. Yeo and D. G. Anstey.
Colonial Insecticide Research Unit, Arusha, Tanganyika.

Earlier papers in this series have described attempts to control tsetse flies by applying insecticides from aircraft. It was concluded (Hocking & Yeo, 1953) that coarse aerosols, with mass median diameters of approximately 100 microns, were more effective than coarse sprays with mass median diameters of 350–700 microns, but that it would not be economically possible to control *Glossina palpalis* (R.-D.), the species associated with dense riverine vegetation, by applications from aircraft. Very promising results were obtained (Hocking & others, 1953) when coarse aerosols were applied to savannah woodland containing *G. morsitans* Westw. and *G. swynnertoni* Aust. In one experiment, where eight applications, each at a nominal dosage of 0·25 lb. of technical DDT (80 per cent. p,p′isomer) per acre, were made at intervals of two weeks, it is possible that *G. morsitans*, and even *G. swynnertoni*, would have been eradicated if the treated woodland had been isolated effectively enough to prevent immigration of flies. In another area, where a similar series of applications was made with BHC, the nominal dosage for each application being 0·25 lb. of crude BHC (12 per cent. γ isomer) per acre, the reductions of fly populations were less spectacular, but these less favourable results were not attributed to a lesser effectiveness of the BHC, but to a combination of circumstances that led to a less effective series of applications.

Several factors were considered to have reduced the effectiveness of the applications in the two experiments, quite apart from immigration which removed any possibility of eradication in the area treated with DDT. The aerosols were produced by allowing the insecticidal solutions to flow, under gravity, into modified exhaust systems of the engines of the aircraft; approximately 20 per cent. of the insecticide was thermally decomposed, and the emission rate fell considerably as the storage tanks emptied, so that wide variations in nominal dosages occurred during each sortie. It is also likely that much of the insecticide was contained in droplets that were too large to penetrate effectively into the resting places of the tsetse flies. Furthermore, the aerosols were not applied during the most suitable meteorological conditions of high temperature inversion and low wind speed (Yeo & Thompson, 1953, 1954), with the result that concentrations of aerosol near the ground were reduced. In the area treated with BHC an incomplete knowledge of the distribution of flies within the treated woodland, and a narrower overlap between successive sorties upon adjacent areas, also reduced the effectiveness of the applications.

It was felt that the eradication of tsetse flies from a savannah habitat was possible, and could be achieved without any increase in the nominal dosage or the number of applications, if sufficient attention was paid to the factors mentioned above, and if there was no possibility of immigration of flies into the treated woodland. A new installation was therefore fitted to the aircraft, by which the aerosol was produced by emitting the solution under pressure through fine nozzles. Thermal decomposition of the insecticide was thus avoided, and a constant emission rate was obtained; there was, however, a disappointingly small change in the sizes of the droplets. A landing strip was constructed near the experimental block, so that sorties could be carried out during the most suitable meteorological conditions, which in the tropics occur during a short period after dawn, and occasionally for a shorter period before dusk. Great efforts were also made to preclude the possibility of immigration of flies, and an extensive preliminary survey was made of the distribution of flies within the woodland.

Originally the experiment was to have been carried out during the long dry season, when most of the principal trees would have been leafless. The installation of the new apparatus into the aircraft took longer than was expected, however, and the experiment was so delayed that the applications did not start until the end of September 1950, and they continued until early in January 1951; the short rains started in November 1950, and the later applications were made when many of the principal trees had fully flushed. Accidentally, and possibly unfortunately, an opportunity was thus provided for studying the influence of varying leaf cover upon the effectiveness of the applications.

Description of the Area.

The experiment was carried out at Kikore in the Central Province of Tanganyika. A general description of the district has been given in a previous paper (Hocking & others, 1953). The treated woodland, known as the Galapo Block, was situated approximately at Latitude 04°18′ South and Longitude 35°55′ East, and had been used previously for control catches of flies; it was just north of the woodland treated in 1949 with DDT. The block was roughly rectangular in

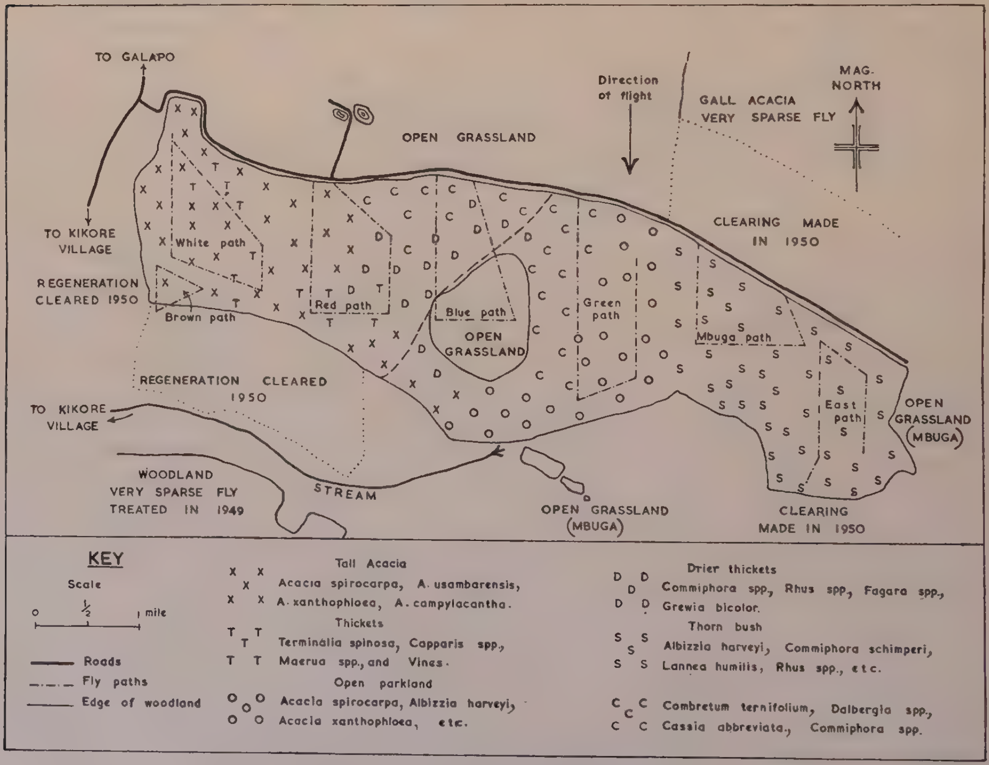

TO GALAPO
Direction of flight
GALL ACACIA VERY SPARSE FLY
MAG. NORTH
OPEN GRASSLAND
TO KIKORE VILLAGE
CLEARING MADE IN 1950
White path
REGENERATION CLEARED 1950
Red path
Blue path
Green path
Mbuga path
OPEN GRASSLAND
Brown path
REGENERATION CLEARED 1950
East path
OPEN GRASSLAND (MBUGA)
TO KIKORE VILLAGE
WOODLAND VERY SPARSE FLY TREATED IN 1949
STREAM
OPEN GRASSLAND (MBUGA)
CLEARING MADE IN 1950
KEY
Scale
0 ½ 1 mile
Roads
Fly paths
Edge of woodland
Tall Acacia
Acacia spirocarpa, A. usambarensis, A. xanthophloea, A. campylacantha.
Thickets
Terminalia spinosa, Capparis spp., Maerua spp., and Vines.
Open parkland
Acacia spirocarpa, Albizzia harveyi, Acacia xanthophloea, etc.
Drier thickets
Commiphora spp., Rhus spp., Fagara spp., Grewia bicolor.
Thorn bush
Albizzia harveyi, Commiphora schimperi, Lannea humilis, Rhus spp., etc.
Combretum ternifolium, Dalbergia spp., Cassia abbreviata., Commiphora spp.

Fig. 1.—Detailed map of the experimental block of woodland.

shape and was two miles wide and seven miles long, the long axis extending eastwards from the foot of the escarpment and Ufiome Mountain. The presence of the higher ground to the west resulted in a greater rainfall and better soil in the western part of the block, and bands of woodland communities tended to occur; these ran parallel to the escarpment and became progressively more xerophytic the farther east they occurred. A detailed map of the treated area is given in fig. 1; the main vegetation communities are shown, and the map indicates the paths upon which catches of flies were made, roads, clearings, and other relevant details.

The isolation of the treated woodland.

Originally the Kikore district had been covered with a continuous belt of woodland, running roughly parallel to the western escarpment and extending for a few miles eastward into the plains. During recent years, however, extensive sheer clearings had been made in the area, which greatly reduced the amount of work required to isolate the block effectively from nearby fly-infested areas, and thus remove the possibility of immigration.

During 1948 and 1949 the area to the north of the Galapo Block had been cleared to a depth of several miles, except in the east where there was a tongue of woodland extending northward into a stand of very scattered gall acacia. This tongue was removed by us early in 1950, making a sheer clearing one mile wide; extensive searches in the scattered gall acacia yielded only an occasional *G. swynnertoni*. The eastern part of the block faced on to an open plain which was in no place less than two miles wide. The eastern end of the southern side of the block had originally extended southward as a narrow tongue of light woodland, to an area sparsely inhabited by *G. swynnertoni*; a clearing two miles wide was made through this tongue. The central section of the southern side faced on to a very wide plain, while its western end was separated from the North Block, the area treated in 1949 with DDT (Hocking & others, 1953), by a sheer clearing which was 1·5 miles wide when all regeneration had been slashed back; there were a few *G. morsitans* and *G. swynnertoni* in the North Block. The western side of the block had originally been separated from the *Isoberlinia-Brachystegia* community on the hillsides, where there was a large population of *G. morsitans*, by a clearing which in places had been only one mile wide. Some of the hillside woodland was cut down, and regeneration was slashed, so that at no place along this side was the clearing less than 1·5 miles wide, and for most of its length it was considerably wider.

The treated woodland was thus surrounded by clearings which were at least one mile where the risk of immigration was slight, and which were at least 1·5 miles wide where there were nearby concentrations of flies. Obviously the wider the clearings the smaller is the possibility of immigration of flies, but any further extension of the clearings in this case would have involved a considerable expenditure.

Flora.

In fig. 1 names have been given to the paths upon which catches of flies were made, and for convenience these will be used to refer to the various parts of the block.

The vegetation was most profuse and massive in the area covered by the Brown and White Paths. The dominant trees of the overstorey were *Acacia spirocarpa*, *Acacia usambarensis*, and giant *Acacia xanthophloea* which were occasionally 100 ft. tall. The general level of the top of the canopy was 60 to 70 ft. Other trees in the overstorey were *Ficus sycomorus* and *Acacia campylacantha*; some large specimens of the latter species occurred but usually it was a tree of medium size and was found near the Brown Path. Beneath the overstorey a dense growth of grass and shrubs grew during the rains to a height of 4 ft., and there were areas of dense, deciduous shrubs, particularly along the eastern arm of the White Path. Much of the undergrowth was thinned out by the annual fires which swept through the block, but the shrubs of *Maerua* spp., *Capparis prunicarpa*, and *Grewia* spp., were left. Where the grass was dominant there were scattered shrubs of *Bauhinia thonningii.*

The north-western part of the area covered by the Red Path was relatively open; *Acacia spirocarpa* grew there, and occasionally *Acacia sieberiana* was found on red soil. The south-western part of this section of the block contained patches of dense thicket; typically these had a central tree of medium-sized *Acacia usambarensis*, and contained *Carissa tetramera*, *Capparis kirkii*, *Maerua* spp., and *Terminalia spinosa.* The soil was brown, with a humus of unburnt leaves. The eastern part of the path passed over a poorer, red eluvial soil, and there was a badly defined ecotone with the drier thickets which consisted of *Commiphora schimperi*, *Grewia bicolor*, *Fagara* spp., and *Dalbergia melanoxylon.* There was also a mixed stand of *Acacia spirocarpa*, *Acacia usambarensis* and *Combretum-Dalbergia-Cassia* spp.

The north-western part of the Blue Path passed through a *Combretum-Cassia* community, which contained trees of *Combretum ternifolium*, *Commiphora spiculatum*, *Dalbergia melanoxylon*, *Dalbergia stuhlmannii*, *Commiphora schimperi*, *Cassia abbreviata*, and *Albizzia* spp. Within a short distance to the south the ground sloped away to the stream which flowed from Kikore village, and an area of broken thicket began. The thickets consisted of the larger trees *Commiphora schimperi* and *Acacia usambarensis*, and included *Grewia bicolor*, *Fagara* spp., *Acacia pennata*, *Acacia mellifera*, *Ziziphus* sp., *Maerua* spp., *Capparis kirkii*, *Cissus* sp., *Strychnos* sp., and others. The thickets were interspersed with *Cassia* sp., *Dalbergia* spp., and *Commiphora* spp. The southern part of the path crossed a small plain of " black cotton-soil " in which there were a few scattered *Acacia xanthophloea.* East of the Blue Path the thickets soon disappeared, and the *Combretum-Cassia* community continued up to the Green Path.

Most of the area covered by the Green Path was open parkland, with short grass and scattered trees of *Sclerocarya birrea* var. *multifoliolata*, *Albizzia sericocephala*, *A. harveyi*, *Acacia spirocarpa* and *Acacia sieberiana.* There were outcrops of white, concretionary, limestone cement through the grey soil.

" Dry thornbush " covered most of the eastern part of the block. The trees were shorter and more numerous than in the parkland of the Green Path. In many places the dominant species was *Albizzia harveyi*; other trees were *Commiphora schimperi*, *Lannea humilis*, *Lannea stuhlmannii* and *Acacia spirocarpa*, and near the seasonal waterholes the shrubs *Rhus* spp., *Ehretia teitensis*, *Fagara chalybea*, *Maerua* spp., *Acacia pennata*, *Acacia mellifera*, *Ormocarpum trichocarpum*, *Capparis tomentosa* and others were found. The eastern boundary of the block was very open, and contained separate clumps of *Albizzia harveyi*, *Lannea humilis* and *Commiphora schimperi.*

The flushing of the principal vegetation types.

It was realised that the amount of leaf cover would increase during the period covered by the applications, and a record was therefore kept of the leaf growth of the more important trees and shrubs. The details are given in Appendix 1. In the western part of the block, the trees began to flush late in October, and by the end of the second week in November the leaves were fully expanded. In the area covered by the Blue and Green Paths flushing began in early November, and was nearly complete by the end of the month. Leaf development was more gradual in the eastern part of the block, and took place during November and December, although *Lannea humilis* was in full leaf by early December.

Fauna.

There were two main groups of animals in the area. One group lived permanently in the block, and was confined to the western section of woodland, whereas the other group moved between the block, the surrounding grassland and nearby fly-infested areas.

In the acacia woodland of the White Path, greater kudu, waterbuck and bushbuck were often seen, and during the rains buffalo were also found. A small herd of impala lived in the more open acacia woodland of the Red Path, and there was a second herd which lived in the area between the Red and Blue Paths and which frequently fed in the afternoons in the open grassland north of the treated woodland. Many baboons and monkeys lived in the western part of the block.

The rest of the game was migrant. During the long rains that ended in May 1950, herds of hartebeest, giraffe and zebra were seen throughout the woodland; the numbers of animals increased immediately after the end of the rains, and wildebeest, eland, roan antelope and oryx were seen, although the oryx were always confined to the eastern boundary of the block. Most of this migrant population was in fact found east of the Blue Path, but the Kikore stream, which flowed for only two miles beyond the village during the applications, was visited at night by animals that moved westwards to it for water. The short rains started in November 1950, and the game population then fell rapidly. The herds of roan antelope, eland, and many other animals left the block and only a few of them had returned before early January 1951, when the insecticidal applications were completed.

The distribution of tsetse flies.

Three species of tsetse flies lived in the Galapo Block: *G. morsitans*, *G. pallidipes* and *G. swynnertoni.* There were no other areas near the block where *G. pallidipes* was to be found, so that a control catch was not possible for this species. Control catches of *G. morsitans* were made in the *Isoberlinia-Brachystegia* woodland growing upon the slopes of the western escarpment, and the South Block, which had been treated with insecticides in 1949 (Hocking & others, 1953), was used for control catches of *G. swynnertoni*. Neither of these areas closely resembled the Galapo Block, so that the catches in them were not entirely satisfactory as controls but more suitable areas did not exist.

Simultaneous catches of *G. morsitans* and *G. swynnertoni* were made in the usual fashion by two African assistants; bait cattle were driven along the paths to catch *G. pallidipes*, since this species does not come readily to man alone. The number of non-teneral male flies caught per 10,000 yd. of search, which is known as the " apparent density " (Swynnerton, 1936), is given in Table I; the figures refer to the period July to September 1950.

It is evident that *G. morsitans* and *G. pallidipes* were confined almost entirely to the western part of the block, and were rarely caught east of the Blue Path. The greatest concentrations of *G. morsitans* occurred near the eastern part of the White Path, where there were dense shrubs, creepers and vines; the population density decreased rapidly towards the east and on the Blue Path it was only one-fifth of the density along the White Path. Very few *G. morsitans* were caught near the thickets along the Red Path, and catches were also low in the small flood plain on the Blue Path. In the densely-shrubbed areas along the White Path the population density of *G. pallidipes* was also high; it was high near the thickets of the Red Path, where *G. morsitans* was scarce. The early searches revealed that no *G. pallidipes* was caught except upon the White, Red, Blue and Green Paths, and in the later searches these four were the only paths along which the cattle were driven. The greatest concentrations of *G. swynnertoni* were in the eastern part of the block, notably near the Mbuga Path, but this species occurred in appreciable numbers as far west as the Red Path, and a few flies were usually caught upon the Brown and White Paths.

Attempts were made to estimate the populations of flies by marking flies with paints of various colours (Jackson, 1948) but a reasonable estimate was possible only for *G. morsitans*, of which a total of of 10,000 non-teneral males was estimated to live in the block prior to the applications.

TABLE I.

The apparent densities of flies in the various parts of the woodland and in the areas used as controls.

Place	Apparent densities of		
	G. morsitans	*G. pallidipes*	*G. swynnertoni*
The treated woodland			
Brown Path	225	0	3
White Path	310	91	1
Red Path	109	47	5
Blue Path	61	34	10
Green Path	2	1	29
Mbuga Path	1	0	79
Eastern Path	0	0	31
Control areas			
Hillside	650	—	—
South Block	—	—	6

The daily maximum and minimum temperatures were measured in a small meteorological screen which was set up near Kikore village. The arithmetic mean of the maximum and minimum temperatures over a period was assumed to be a sufficiently accurate measure of the average temperature, and it was used to calculate pupal periods by substituting it into an equation obtained by Jackson (1949). The temperatures, and the calculated pupal period for females, are given in Table II; pupal periods for males are approximately 5 per cent. longer than for females (see Jackson, 1949).

The temperatures and pupal periods are probably only approximately correct, but it is improbable that the true pupal periods exceeded 35–40 days during the period of the applications.

TABLE II.

Average maximum and minimum temperatures, and calculated pupal periods for females.

Month	Average maximum temperature (°F.)	Average minimum temperature (°F.)	Pupal period (days)
1950			
July	79·9	53·5	52
August	80·1	55·0	49
September ..	—	—	—
October	89·0	58·2	34
November	86·8	62·3	32
December	89·2	62·0	30

The Control of Dosage and Field Methods.

A 10 per cent. w/v solution of technical DDT (80 per cent. p,p′ isomer) was used, the solvent consisting of equal parts by volume of Shell Power Kerosene and Shell Diesoline. The solution was prepared by heating the solvent to approximately 110°F. and then adding the DDT powder, which dissolved readily. Chemical analyses showed that the amount of DDT in the cool solution was never very different from the required value. In our earlier experiments (Hocking & others, 1953), the solvent was a mixture of Shell Power Kerosene and Shell Furnace Oil; the Diesoline was substituted for the Furnace Oil to reduce the amount of sludge in the solution, and the blocking of the fine nozzles through which the solution was emitted.

In the western parts of the block, where the canopy was high and relatively dense, and where there were many dense thickets, greater nominal dosages were used than in the more open eastern parts. The aircraft was flown at a speed of 100 m.p.h. In the area covered by the Brown and White Paths, an emission rate of 8 gallons per minute and a swathe width of 55 yd. were used, thus giving a nominal dosage of 0·24 lb. of DDT per acre. An emission rate of 8 gallons per minute was also used in the area covered by the Red and Blue Paths, but here the swathe width was increased to 70 yd. so that the nominal dosage in this part of the block was 0·19 lb. of DDT per acre; in the remaining, eastern, part of the block an emission rate of 7 gallons per minute and a swathe width of 70 yd. were used, giving a nominal dosage of 0·165 lb. of DDT per acre.

Successive sorties were overlapped. The first few runs of a sortie were used to treat again the area that had been treated by the last few runs of the previous sortie, and they were spaced at intervals equal to 1·5 times the swathe width used for the main part of the sortie. This overlap has been discussed previously (Hocking & others, 1953); here it was 500–600 yd. wide, which was considered to be sufficient to prevent the escape, by movement between sorties, of an appreciable number of flies. Considering the block as a whole, and including the insecticide used in the overlaps, each application was carried out at a nominal dosage of nearly 0·25 lb. of technical DDT per acre, equivalent to 0·25 gallons of solution per acre.

Seven complete applications were carried out over a period of approximately 15 weeks; the first application started late in September 1950, and the last application was completed early in January 1951. Up to the fourth application the interval between applications was 14 days; the fifth and subsequent applications were carried out after intervals of 16 days. For any particular section of the block the applications covered a period of 90 days, that is, at least two, and possibly nearly three, pupal periods.

The production and drop spectrum of the coarse aerosol.

The aircraft installation consisted essentially of storage tanks, a pump, a boom fitted with nozzles, and various pipes and connections. The solution flowed under gravity to the pump, which forced it under pressure into the boom and then through the nozzles.

Two banks of storage tanks were fitted within the fuselage of each aircraft, between the spars of the mainplanes. They were made of light alloy, and could be isolated from the rest of the system by means of a Saunders cock which was fitted in the connecting pipe between the two banks. From the cock a pipe led down to the gear pump, directly coupled to a small wooden windmill which was driven directly by the slipstream. This windmill had four blades and was 15 in. in diameter. It rotated at approximately 2,000 r.p.m. when the aircraft's airspeed was 110 m.p.h., and was fitted with brake shoes which were operated, through Bowden cables, by a ratchetted lever in the cockpit. The spray boom, made of light alloy, was just over 52 ft. long and was approximately 4 ft. shorter than the total wing span of the aircraft; it had an internal diameter of 1·5 in. It was fitted to the lower surface of the wing and fuselage so that it was approximately 12 in. below the under surface of the wing, and was parallel to the rear spar. Along its length 24 Bray " 0 " nozzles (cross sectional area of orifice = 0·0078 sq. cm.) were spaced at intervals of 2ft., except immediately behind the two engine nacelles where the interval was 4 ft. This boom was slightly different from that used in the work described by Yeo & Thompson (1953, 1954) where 24 Bray " 1 " nozzles were spaced along a boom only 26 ft. long. From between the pump and the boom a pipe led back to the bottom of the storage tanks, through a relief valve which was of the spring-loaded-plunger type. This valve could be used to vary the pressure built up in the boom, and therefore the rate of emission, but the adjustment was possible only when the aircraft was on the ground.

With a boom pressure of 150 lb. per sq. in. and 24 Bray " 0 " nozzles the emission rate was 10 gallons per minute. The lower emission rates used in the applications to the Galapo Block were obtained by reducing the number of nozzles. The Saunders cock was kept closed until the aircraft arrived over the experimental area; it was then opened and the liquid was able to flow to the pump. Emission was controlled by the brake fitted to the windmill, and took approximately five seconds to reach a constant rate at the beginning of the first run of each sortie, and a second or so for subsequent runs.

The drop spectrum of the aerosol was assessed in two ways: by counts upon glass plates, coated with magnesium oxide, which were placed upon the ground, and by counts and colorimetric estimations of samples taken with cascade impactors (May, 1945). The distributions of the volume of liquid over the droplet ranges are shown in fig. 2, where (a) shows the distribution obtained from the counts upon the oxide-coated plates placed upon the ground, and (b) shows the distribution obtained by size counts, again using magnesium oxide, of the samples with the cascade impactors. For convenience the equivalent distributions for the installation used in previous work (Hocking & Yeo, 1953; Hocking & others, 1953) are given by (c) and (d). Colorimetric estimations of the deposits upon the various slides of the cascade impactors indicated that approximately 10 per cent. of the DDT in samples collected by the impactors was contained in droplets less than 13 microns in diameter, compared with a not very reliable estimate of 5 per cent. below 13 microns for the old installation.

The graphs show that the boom installation produced a slightly different drop spectrum from that of the old installation. A smaller proportion of the insecticide was contained in droplets greater than 100 microns in diameter; and apparently fewer droplets were less than 13 microns, but since the colorimetric estimations indicated that more DDT was contained in these smaller sizes too much reliance should not be placed upon the size distribution obtained with the cascade impactors, particularly since magnesium oxide is not an ideal medium with which to detect the very small droplets of the spectrum. It seems reasonable to infer, however, that the boom installation produced a coarse aerosol that contained more of the insecticide in droplets of diameters ranging from 10 microns to 50 microns. Unpublished work has shown that these are the most effective droplets for penetrating into resting sites and there depositing upon the flies. There was therefore some improvement in the drop spectrum.

It is now considered that the procedure adopted in previous work (Hocking & Yeo, 1953) for calculating the complete spectrum, where the distributions obtained by the two assessment methods were equated over the range of sizes from 40 microns to 50 microns, had little justification, and so the exact form of the droplet distribution is unknown. It must lie somewhere between (a) and (b) of fig. 2, and the mass median diameter is probably approximately 60 microns.

Field methods and organisation.

Two aircraft were used to carry out the applications. They were Avro Ansons (Mark I), low-wing, twin-engined monoplanes fitted in this case with engines rated at 350 h.p. The landing strip cost very little to prepare (approximately £30) and was eight miles south of the Galapo Block. It was located partly upon "black cotton-soil" and became unusable when there was heavy or prolonged rain; fortunately the distribution of rainfall during the entire series of applications was such that only on four occasions was it necessary to use the permanent runway at Arusha, 90 miles to the north. Insecticides and solvents were transported by road from Arusha to Kikore, where the solution was prepared; an emergency supply of solution was also kept at Arusha.

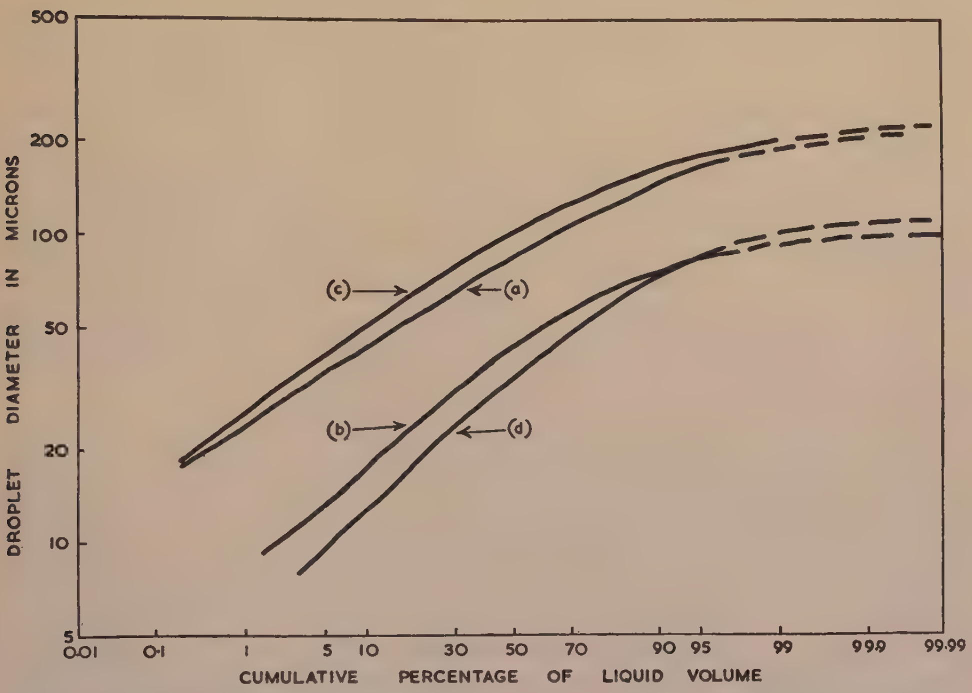


Fig. 2.—Drop spectra of the boom installation, and of the installation used in previous work.

During the earlier applications each aircraft normally carried 110 gallons of solution, but this was later increased to 130 gallons. Normally only one sortie was carried out each day, during the first hour or so after dawn; this is the period of the day associated with the most stable atmospheric conditions. Each complete application took 9 to 11 sorties. Previous observations in the area had shown that generally the wind blew from an easterly direction, although occasionally katabatic effects arising from the high ground to the west produced winds blowing from a westerly direction. The runs were therefore made from north to south, at right angles to the general wind direction and conveniently along the shortest dimension of the block. The beginning of each run was indicated to the pilot with a white banner, and each run was completed by flying upon a compass course.

The compass course was determined in the following manner. The required track was 180°M. The compass of each aircraft was "swung" so that deviations from true magnetic bearings were determined and both aircraft could be flown on the same true magnetic course. Before each sortie a preliminary run was made, at a height of approximately 50 ft. above the trees and at a compass course which in the absence of drift would give a track of 180°M.; during this run the radio officer measured the drift due to the wind by means of a conventional drift sight. The compass setting was then changed to allow for this drift, so that the aircraft could be flown on a track of 180°M. An observer on the ground took readings of wind speed and direction, to act as a check upon the accuracy of the drift measurement; only rarely were the two estimates of drift seriously different, and when this occurred it was usually attributable to an error in the somewhat difficult observation made by the radio officer, and the discrepancy was removed by a further preliminary run. Both aircraft used the same correction for drift. During the runs of a sortie the radio officer continued to measure drifts, so that any large variations in wind speed and direction could be allowed for. In general, however, no changes were made in the compass setting after the first run, except when the wind speed and direction changed considerably; the slight variations in track from day to day were amply allowed for in the overlap between sorties. This flying procedure was considered to be superior to that used in our previous work, where the pilot attempted to set his compass upon the required bearing while making a low run over two markers placed upon the ground along the required direction.

The system of using only one marker, and carrying out runs on a corrected compass course, was only possible because the runs were relatively short (approximately 2½ miles long), and because there was a wide overlap of 500–600 yd. between successive sorties. The accuracy of the tracking was checked by measuring the swathe spacing at the ends of the runs farthest from the marker. On the occasions when this was done the tracking of each aircraft showed remarkable consistency, although sometimes there were differences of ½ to ¾° between the tracks of the two aircraft, and between sorties differences were sometimes of the order of 2°. With the relatively short runs of this experiment such errors were not very important, although they may have led to slightly more uneven dosages at the far ends of the runs and often to a slightly reduced overlap there. They would become important with long runs, however, and without an overlap some areas would probably not be treated effectively. Counts of droplet numbers were made near the markers and near the other side of the woodland, and it was found that the standard deviation of the mean density of numbers of droplets were not appreciably different in the two places, even on one occasion when the spacing of the runs of one aircraft had an error of 30 yd. These counts truly tested the distribution of droplet numbers, not dosages of DDT, but it is improbable that the slight inaccuracies of flying led to important dosage variations, at least not in the droplet sizes that are considered to be mainly responsible for killing resting flies.

The aircraft were flown and maintained by seven Europeans: three pilots, two radio officers, and two qualified engineers. The ground work involved in the experiment was carried out by six Europeans and approximately 20 Africans. The staff was much larger than would be required for routine operations, and much of its time was taken up with problems not directly concerned with the applications. As was shown in later work, the operation and maintenance of the aircraft, and the mixing and loading of insecticide, can be adequately dealt with by two pilots, two engineers, one radio officer, and 6 to 8 African assistants, provided that the landing strip does not require much maintenance. The staff in the experimental area would depend upon the survey work that was considered necessary; one experienced European and 4 to 6 African assistants would be sufficient in most cases.

TABLE III.

Average catches of non-teneral males, and of all flies, for one complete search.

Date	The Galapo Block						The Control Paths			
	G. morsitans		*G. pallidipes*		*G. swynnertoni*		*G. morsitans*		*G. swynnertoni*	
	Non-teneral males	All flies	Non-teneral males	All flies	Non-teneral males	All flies	Non-teneral males	All flies	Non-teneral males	All flies
Jan. 1950	581	641	—	—	—	—	284	311	35	44
Feb.	561	646	—	—	—	—	—	—	37	53
March	598	649	—	—	—	—	296	334	35	46
April	667	725	—	—	—	—	360	398	40	61
May	704	767	169	310	—	—	312	353	52	70
June	373	439	289	466	—	—	416	446	26	42
July	468	556	152	303	76	84	277	304	20	32
Aug.	432	488	141	225	82	98	311	354	20	28
Sept.	360	390	65	86	76	92	301	320	22	26
	FIRST APPLICATION									
Period of the applications (late Sept. to early Jan.). See p. 591.	8	11	1	2	(10)*	(21)*				
	8	21	1	3	6	16	298	339	14	18
	SECOND APPLICATION									
	0	0	0	0	0	0				
	3	12	0	0	3	11				
	THIRD APPLICATION									
	0	0	0	0	0	1				
	5	11	0	0	1	3				
	FOURTH APPLICATION						325	358	7	13
	0	2	0	0	2	2				
	0	1	0	0	3	5				
	FIFTH APPLICATION									
	0	0	0	0	0	1				
	2	2	0	0	0	2				
	1	3	0	0	2	3				
	SIXTH APPLICATION									
	0	0	0	1	1	2	397	431	21	26
	0	0	0	0	1	2				
	(0)	(0)	0	0	0	1				
	SEVENTH APPLICATION									
	0	0	0	0	0	0				
Jan. 1951	2·7	4·2	0·2	0·4	2·8	5·3	360	380	21	33
Feb.	4·0	6·3	0·2	0·2	5·7	6·7	406	423	21	26
March	13·0	17·7	0	0·3	5·3	6·3	356	384	45	51
April	11·0	16·0	0·5	0·5	8·5	9·5	339	366	22	28
May	12·5	17·0	0	0·5	4·0	7·0	295	324	18	23
June	13·5	16·5	0·5	1·0	7·5	8·5	342	365	21	25
July	14·5	16·5	0	0	2·5	3·5	315	355	22	27
Aug.	5·7	6·5	0·5	0·5	3·3	5·2	353	388	10	12
Sept.	5·0	6·5	0	0	2·2	3·0	322	363	3	6
Oct.–Dec.	5·1	6·6	0	0	1·0	1·6	285	311	5	7
Jan.–Mar. 1952	6·0	6·3	0	0·3	1·3	1·3	252	275	6	9
Apr.–June	4·3	5·3	0	0	3·3	4·0	267	288	9	11
July–Sept.	2·3	3·3	0	0	1·7	2·3	215	227	Block destroyed	
Oct.–Dec.	3·0	3·0	0	0	2·0	2·5	115	121		
Jan.–Mar. 1953	5·0	5·5	0	0	1·0	1·0	178	191		
Apr.–June	5·7	6·7	0	0	0·7	1·2	195	216		

---

* One important search was not carried out until six days after an area was treated, and due to a misunderstanding by the pilots a portion of the south-eastern part of the block was not adequately treated.

Entomological Results.

Before the applications started, searches were made each week. Between applications they were made as soon as possible (1 to 3 days) after an area had been treated, and also after 7 to 10 days; and for the later applications a further search was made immediately before an area was treated. During 1951 the searches were usually carried out twice during each month, and in 1952 and 1953 this was reduced to one search each month. The catches are summarised in Table III. To avoid undue complexity in the Table, average catches of non-teneral males and of all flies are given for a complete search during the periods shown in coloumn 1, except during the applications when all searches are recorded.

It is convenient to consider separately the three species of flies.

G. pallidipes.—The catches fell considerably during the three months immediately preceding the applications. Unfortunately it was not possible to obtain control catches of this species, so that it is impossible to state what would have happened to the undisturbed population. It is most improbable, however, that such a large population would have disappeared if the applications had not been made. Before the applications, each complete search, covering 15 miles of path, yielded 80–500 flies; in 1951, the year following the treatments, only 5 non-teneral males and 5 non-teneral females were found in searches totalling 480 miles, and in 1952 and 1953, apart from one fly in January 1952, none of this species has been caught in searches totalling 195 miles. The applications so drastically reduced the population of this species that it has almost certainly died out.

For the other two species, estimations of the effectiveness of the experiment depend to some extent upon whether catches of non-teneral males or of all flies are considered, upon the periods chosen for comparison of pre-treatment and post-treatment catches, and also upon the inclusion of corrections for the control catches. For simplicity, only non-teneral males will be considered; the figures would be slightly different if catches of all flies were considered.

G. morsitans.—Comparing the catches during February and March 1951 with those during August and September 1950, the uncorrected figures give a reduction of 97·8 per cent.; allowing for variations in the control the reduction is 98·2 per cent. If the periods July to September 1950 and January to September 1951 are compared, the figures are, respectively, 97·8 per cent. and 98·1 per cent. The population fell during 1952 and 1953, and in April to June 1953 was only 1·4 per cent. of its pre-treatment level during July to September 1950; this figure becomes 2·1 per cent. when corrected for variations in the control. It is reasonable to assume, therefore, that the applications reduced the population of *G. morsitans* to approximately 2 per cent. of its original level.

G. swynnertoni.—Considering the two periods August to September 1950 and February to March 1951, the uncorrected reduction was 93 per cent.; this figure becomes 95·6 per cent. when control variations are taken into consideration. If the period January to September 1951 is compared with the period July to September 1950, the uncorrected and the corrected reductions are both 93·7 per cent. In April to June 1952, the population was 4·2 per cent. of its pre-treatment level during July to September 1950; corrected for control variations this figure becomes 9·6 per cent. The control block was destroyed in 1952 so that corrections cannot be applied to later catches in the Galapo Block, where by April to June 1953 the population had fallen to only 1 per cent. of its pre-treatment value. It appears that the applications caused a reduction of about 94 per cent. in the population of this species; subsequently the population has fallen very considerably, but probably this can be attributed to a general recession of *G. swynnertoni* in the Kikore district.

Discussion.

The main points that arise from the entomological results are the differences between the reductions of the populations of the three species of flies and the differences between the results of this and previous experiments.

The principal concentrations of *G. morsitans* and *G. pallidipes* were found in nearly the same areas, sufficiently so to say that both species were subjected to the same treatment. If for some reason, for example poor meteorological conditions, the applications had been ineffective in the areas where these species were mainly found, the reduced effectiveness should have been reflected in the catches of both species. In fact the proportionate reduction of *G. pallidipes* was an order of magnitude greater than of *G. morsitans*. The catches of *G. pallidipes* fell considerably before the applications; but then this time of year is usually associated with a decrease, and during the period of the applications a slight increase rather than a decrease would normally have occurred. It is difficult, therefore, to explain the greater reduction of *G. pallidipes* unless this species was easier to kill than *G. morsitans*. There are several possibilities. The two species may have different susceptibilities to DDT. It is also possible that *G. pallidipes* collects more insecticide during the applications, either by resting in sites more easily reached by the aerosol, or, being more active during the early morning when the applications were made, by having a greater proportion of its population on the wing and therefore not only readily accessible to the aerosol but also capable of collecting more insecticide by reason of the act of flying. A further possibility is that *G. pallidipes* was at all times confined to the treated woodland, whereas a proportion of the two other species may have been outside the woodland during the treatments. There is, in addition, the fact that immigration of *G. pallidipes* was virtually impossible, whereas such a possibility did exist for the other species; the subsequent fluctuations of the populations of *G. morsitans* and *G. swynnertoni* strongly suggest, however, that immigration of these two species was negligibly small.

A comparison of the results for *G. morsitans* and *G. swynnertoni* is not so simple, because these species were distributed very differently through the woodland, and variations in dosage and in the effectiveness of the applications cannot be immediately eliminated from the discussion. Some order in the data may be obtained if the block is considered in three separate sections. The first section includes the Brown and White Paths, where each sortie was carried out at a nominal dosage of 0·24 lb. of technical DDT per acre and a swathe width of 55 yd.; the second section was covered by the Red and Blue Paths and was treated with a nominal dosage of 0·19 lb. of technical DDT per acre and a swathe width of 70 yd., whereas the third section, covered by the Green, Mbuga and Eastern Paths, was treated with a swathe width of 70 yd. and a nominal dosage of 0·165 lb. of technical DDT per acre. The greatest dosages were thus applied to the areas with the densest and highest vegetation (Brown and White Paths, see p. 587).

Some total catches of non-teneral males in these three sections are given in Table IV. The figures apply to the periods July to September 1950, and January to September 1951, and the Table includes the number of searches. During both periods the control catches of non-teneral males of *G. swynnertoni* were 20 per search, and the respective figures for *G. morsitans* were 297 and 341. The figures of Table IV were used to carry out χ^2 tests of significance, by grouping them into convenient 2 × 2 tables. In the areas covered by the Red and Blue Paths the reduction of *G. morsitans* was significantly greater than for *G. swynnertoni* ($P < 0{\cdot}001$); this significance would increase if control variations were considered. For *G. morsitans* the reduction was significantly greater in the Brown-White area than in the Red-Blue area ($P < 0{\cdot}01$), although this significance disappeared if the catches for July to September 1950, and July to September

1951 were considered. No significant difference was found between the reduction of *G. swynnertoni* in the Red-Blue area and in the Green-Mbuga-Eastern area ($P > 0{\cdot}2$).

These tests of significance suggest that most of the difference between the reductions of these two species may reasonably be attributed to the greater ease with which *G. morsitans* was killed, rather than to any difference that may have arisen because the species were differently distributed through the woodland and were therefore subjected to slightly different applications. This may be qualified by saying that the highest kill was possibly associated with the highest dosage and the narrower swathe width, and with a high population density of *G. morsitans*, and that this slightly increased the reduction of *G. morsitans* relative to that of *G. swynnertoni*.

TABLE IV.

Total catches of non-teneral males in the three main sections of the Galapo Block, for the periods July–September 1950, and January–September 1951.

Species of fly	Period	Number of rounds	Total catches of non-teneral males		
			Brown-White	Red-Blue	Green-Mbuga-Eastern
G. morsitans	July–Sept. 1950	11	3466	1158	—
	Jan.–Sept. 1951	27	132	67	—
G. swynnertoni	July–Sept. 1950	11	17	98	678*
	Jan.–Sept. 1951	27	5	18	82

* Only eight searches were done in this area during this period, and the figure of 678 was calculated.

There is, therefore, significant evidence that the three species are not equally easy to kill with coarse aerosols. As was mentioned previously, this may have been due not only to differences in susceptibility, but also to differences in behaviour and habit which allowed some species to pick up more insecticide. Evidently comparative tests of susceptibility should be made, and it would be most valuable to investigate the resting habits of the three species, and their behaviour response to coarse aerosols.

Two similar experiments have been carried out previously (Hocking & others, 1953), in the areas at Kikore known as the North and South Blocks, and the final reductions were considerably different from those of this experiment. Some catches of non-teneral males in the three experiments are given in Table V. In column 3 is recorded the average catch per search during the month preceding the first application, and column 4 shows how many flies were caught in one search made immediately after the first application; column 5 gives the sum of the catches made on single searches after the second and third applications, while column 6 records the total number of flies caught in similar single searches after each of the subsequent applications—in the North and South Blocks there were eight applications so that column 6 records the total catch on five searches in each of these areas, whereas in the Galapo Block seven applications were made and for this area column 6 therefore represents the sum of catches of four searches.

Except that after the later applications they were relatively higher in the South Block, the catches suggest no very significant differences between the effectiveness of the applications in the three areas. On the other hand, if the catches before and after each complete series of applications are considered, reductions of a particular species were significantly different in the three experiments, and were 94 to 98 per cent. in the Galapo Block (see p. 596), approximately 90 per cent. in the South Block, and greater than 99·5 per cent. in the North Block (Hocking & others, 1953).

TABLE V.

Some catches of non-teneral males in the North, South, and Galapo Blocks.

Species of fly	Block	Number of non-teneral males caught			
		Before applications	After first application	After 2nd & 3rd applications	After subsequent applications
G. morsitans	Galapo	360	8	0	0
	North	427	—	4	1
	South	33	0	0	3
G. swynnertoni	Galapo	76	(2)*	0	2
	North	100	—	4	3
	South	272	11	1	16

* No relevant catch was made upon the Eastern Path, and this figure applies only to the rest of the block.

It is difficult to attribute causes to the differences between the results in the three blocks; so many factors were not common to the three experiments. Previously the smaller reductions in the South Block, compared with those in the North Block, were attributed to " a combination of circumstances which led to less effective applications upon important fly concentrations, more adverse meteorological conditions during the actual sorties, difficulties in treating the area, and an inadequate overlap " (Hocking & others, 1953); and these statements, being qualitative, are sufficient to account for the different results in these two areas. The best applications would have been expected in the Galapo Block, where they were carried out with a wide overlap between sorties and a more suitable drop spectrum, and where the atmospheric conditions were more favourable during the actual sorties.

An important factor might have been the vegetation cover. This was densest in the Galapo Block, where it increased considerably during the later applications. The figures of Table V suggest that the cover was not important there during the earlier applications; it is, however, difficult to assess the effectiveness of the later applications of a series because the catches are then so small and unreliable, and it is possible that the increased cover during the later applications in the Galapo Block did have an important effect which could not be directly determined but which was reflected in the final reductions. This argument is not contradicted by the very large reduction in the population of *G. pallidipes*, provided that the earlier applications were much more effective against this species than against *G. morsitans* and *G. swynnertoni*.

A series of applications that covers three complete pupal periods would be expected to give considerably greater reductions than one covering two complete pupal periods and only part of a third. The average temperatures during the applications in both the North Block and the Galapo Block was between 73°F.

and 74°F., so that in both cases the average pupal period was approximately 33–34 days. In the North Block the applications covered 98 days, therefore possibly three complete pupal periods, whereas in the Galapo Block they covered only 90 days, less than three complete pupal periods, so that the longer series in the North Block may have caused the greater reductions there.

In the preceding paragraphs an attempt has been made to explain the different reductions in the three areas in terms of known variations in field conditions. A simpler explanation may be that the many field variables randomly affect the applications, so that the final reductions, although always high, can never be predicted with certainty, and eradication is the result of good fortune. Some justification for this argument arises from the fact that upon the few occasions when the kill of one application has been assessed a figure of 95 per cent. or more has been obtained, and yet a series of applications, covering at least two pupal periods, has produced on occasions a final reduction that is no greater than the kill of one application, instead of an order of magnitude greater.

With present methods, insecticides, and dosages, it appears that only great reductions, and not eradiction, of populations of tsetse flies can be guaranteed. In the one experiment with *G. pallidipes* the effect of the applications was so great that the small residual population died out. If elimination is essential before an area becomes habitable to livestock, we have demonstrated the feasibility of this only with *G. pallidipes*. There are, however, other points to be considered before deciding whether insecticidal applications would be of value in a particular area.

The results with *G. pallidipes* suggest that if a residual population has a density that is sufficiently small it subsequently dies out. Elimination of *G. morsitans* and *G. swynnertoni* might therefore result in areas where the original population densities were less than in the areas treated so far, even though the applications produced no greater proportionate reductions. Alternatively, an increase in the number of applications, possibly to twelve, would probably so reduce populations in many areas that the flies would finally disappear. A comparable case has occurred in South Africa, where several series of applications have been made over a period of several years, each against a reduced population, and probably the tsetse flies have now been eliminated (R. du Toit, E. B. Kluge & O. G. H. Fiedler, unpublished, 1953).

Although eradication of tsetse flies is obviously the most desirable result of any control measure, it is by no means essential in all cases. For example, it is of interest to record that in the Kikore district there are now large numbers of livestock living around and in the areas treated during our experiments, whereas previously none lived there because of the certainty of outbreaks of trypanosomiasis. A very large reduction in the numbers of flies may prove sufficient for many areas to be opened to settlement; the organised introduction of families would eventually drive out the game and the remaining flies with it. Without a large reduction this introduction of families might be impossible, for fear of loss of the entire livestock population. Our results show that the settlement period can cover a period of several years without fear of any appreciable increase in the numbers of flies; most settlement schemes usually need several years before they are completed. A further important situation in which insecticidal methods would be of value is where an isolated area is infested and, although in itself of no immediate value for settlement, constitutes a threat to neighbouring stock-raising country; this threat would be virtually eliminated by a drastic reduction in the tsetse populations, and would not require eradication since, apparently, small residual populations do not increase.

As is the case with all control measures, the cost is vital in determining whether this particular method will be used. Land in Africa, particularly in tsetse-infested areas, is generally not very productive and therefore of no great economic value except where there is a considerable pressure of population.

Costs must be low, therefore, if the use of insecticides is to compete with other methods of control; they are dependent upon many factors when aircraft are used, the most important of which is the degree to which the aircraft are utilised, and it is perhaps of value to indicate in a crude fashion how they are affected by the various items.

Assuming that eight applications are carried out at a nominal dosage of 0·25 gallons per acre of a 10 per cent. w/v solution of technical DDT, the cost of the insecticide and solvents is approximately 11 shillings per acre and is little affected by transport charges from the nearest railhead. In control rather than experimental work, it is unlikely that the cost of ground staff, transport and incidental items would amount to more than two shillings per acre. The remaining costs are incurred in the operation and maintenance of the aircraft, and are of two types. One type, known as the standing charge, is the cost of maintaining the aircraft and paying the salaries of the aircrews and engineers; the other is the running charge, which is the expense incurred during the actual flight of the aircraft, and is therefore mainly concerned with the price of petrol, oil, and minor spares. For one Anson aircraft the two charges are as follows:—

Standing charge	£11,000 per annum
Flying charge	£9 per hour.

With two such aircraft, and present methods and dosages, an area of approximately 18 sq. miles can be treated with eight applications during a period of four months, and the treatment would involve a total of approximately 200 hours of flying; the standing charge would amount to £7,300 and there would be £1,800 for flying charges. Thus most of the expense of the aircraft would arise from the standing charge, and the total cost per acre for the aircraft would be 16 shillings per acre. The total cost of the applications would be 29 shillings per acre or approximately £1,000 per sq. mile. This figure compares favourably with sheer clearing of woodland, but is more expensive than certain types of discriminative clearing or the killing of game. Sheer clearing is, of course, the certain way to eliminate tsetse flies.

Summary.

An experiment is described where applications of a coarse aerosol were made to savannah woodland containing the tsetse flies, *Glossina morsitans* Westw., *G. swynnertoni* Aust. and *G. pallidipes* Aust.

Seven applications were made, each at a nominal dosage of 0·25 lb. of technical DDT per acre and 0·25 gallons of solution per acre. The applications in any particular part of the treated woodland covered an interval of 90 days, or rather more than two pupal periods.

The coarse aerosol was produced by emitting the insecticidal solution under pressure through fine nozzles fitted to a boom. It had a mass median diameter of approximately 60 microns, and droplet diameters varied from a few microns to approximately 200 microns.

The population of *G. pallidipes* was so drastically reduced that it has subsequently died out. The reduction of *G. morsitans* was approximately 98 per cent., and of *G. swynnertoni* approximately 95 per cent. The differences between the reductions are attributed mainly to differences between the ease with which the three species can be killed. It is pointed out that this is not necessarily equivalent to differences in susceptibility.

Comparisons are made with previous experiments, and the different results of the various experiments are difficult to explain satisfactorily. The increased cover in savannah areas during the leafy period may have reduced the effectiveness of the applications, and the total periods covered by the various series of

applications were probably also important. Random effects, leading to ineffective treatments, may also be important.

Costs are discussed.

Acknowledgements.

The authors are grateful to the staff of Messrs. Airwork, Ltd., for the operation and maintenance of the aircraft. We are also grateful to Messrs. D. Lovemore and J. Gledhill, who at different times helped with the field work, and also to other members of this unit, particularly Messrs. S. Znatowicz, G. F. Burnett, and G. C. Dauber. Dr. C. H. N. Jackson, of the East African Tsetse and Trypanosomiasis Research and Reclamation Organisation, gave much valuable advice. The aircraft installation was designed and fitted by the Engineering Section, Ministry of Supply, Porton, England.

The work was directed by the Colonial Insecticides Committee and was paid for from the Colonial Development and Welfare Fund.

References.

Hocking, K. S. & Yeo, D. (1953). Bull. ent. Res., **44,** pp. 589–600.

Hocking, K. S., Parr, H. C. M., Yeo, D. & Anstey, D. (1953). Bull. ent. Res., **44,** pp. 627–640.

Jackson, C. H. N. (1948). Ann. Eugen. Lond., **14,** pp. 91–108.

Jackson, C. H. N. (1949). Biol. Rev., **24,** pp. 174–199.

May, K. R. (1945). J. sci. Instrum., **22,** p. 187.

Swynnerton, C. F. M. (1936). Trans. R. ent. Soc. Lond., **84,** 579 pp.

Yeo, D. & Thompson, B. W. (1953). Nature, Lond., **172,** pp. 168–169.

Yeo, D. & Thompson, B. W. (1954). Bull. ent. Res., **45,** pp. 79–92.

APPENDIX 1.

The leaf growth upon important trees in the Galapo Block.

Tree	First flush of leaves	In full leaf
Acacia campylacantha	25.x.52	15.xi.52
Acacia spirocarpa	27.x.52	17.xi.52
Acacia usambarensis	15.x.52	5.xi.52
Acacia xanthophloea	15.x.52	10.xi.52
Albizzia harveyi	10.xi.52	30.xi.52
Albizzia sericocephala	10.xi.52	30.xi.52
Bauhinia thonningii	10.xi.52	10.xii.52
Cassia abbreviata	10.xi.52	25.xi.52
Combretum spp.	10.xii.52	30.xii.52
Commiphora spp.	30.xi.52	25.xii.52
Dalbergia melanoxylon	5.xii.52	25.xii.52

Tree	First flush of leaves	In full leaf
Dalbergia stuhlmannii	15.xi.52	5.xii.52
Lannea humilis	30.x.52	5.xii.52
Rhus spp.	30.x.52	20.xi.52
Sclerocarya birrea	10.xi.52	25.xi.52
Thylachium, *Cadaba* and *Maerua* spp.	In leaf during the entire series, with new leaves appearing from approximately 20.xi.52.	

AIRCRAFT APPLICATIONS OF INSECTICIDES IN EAST AFRICA.

VII.—AN EXPERIMENT AGAINST THE TSETSE FLIES, *GLOSSINA MORSITANS*, WESTW. AND *G. SWYNNERTONI* AUST., IN THE RAINY SEASON.

By K. S. Hocking, G. F. Burnett and R. C. Sell. D
Colonial Insecticide Research Unit, Arusha, Tanganyika.

(Plate XLI.)

The previous paper in this series (Hocking & others, 1954) describes the attempted elimination of the tsetse flies, *Glossina morsitans* Westw., *G. swynnertoni* Aust. and *G. pallidipes* Aust., from an area of savannah woodland using an oil-DDT solution applied as a coarse aerosol. It was concluded that the coming into leaf of the trees was the principal reason for incomplete eradication. The experiment described in this paper was necessarily planned before the end of the previous one, when it was apparent that the new equipment was proving more successful than the exhaust generator previously used, which had obtained a reduction of over 99 per cent. in the fly in 1949 (*l.c.*). The object was to test the method and equipment in less advantageous conditions by using them in the season when the bush was in full leaf. Unfortunately difficulties arose in that only one aircraft was available and the rains were quite exceptionally heavy and prolonged. The experiment started in late January and continued until early May.

Description of Area.

Vegetation.

The block was that treated with the DDT exhaust-generated aerosol in 1949 (Hocking & others, 1953). It is situated near Kikore, Central Province, Tanganyika Territory (Lat. 04°23′S., Long. 35°50′E.) and about 90 miles by air from the all-weather airfield at Arusha (Lat. 03°22′S., Long. 32°28′E.). It has always been known as the "North Block" although immediately south of the Galapo block described and figured in a later paper (Hocking & others, 1954). The vegetation is described and mapped in the paper on the 1949 experiment, which was carried out when the bush was quite leafless, but during the operation here discussed all the trees were in heavy leaf (Pl. XLI, figs. 1 & 2).

Game.

Before and during the early part of the operation a fair amount of game was reported in the block, including zebra, roan antelope, eland, Coke's hartebeest, wart-hog and especially impala. Several herds of impala lived permanently in the block and were often found between the bush and the tsetse-infested hills, sometimes above the road, and may have carried an occasional fly into the block. From February onwards practically no animals other than impala were seen in the area.

Fly distribution.

The bush contained comparatively small numbers of both *G. morsitans* and *G. swynnertoni*. The *G. morsitans* lived principally in the two areas of *miombo*

(*Isoberlinia globiflora*, *Brachystegia microphylla*, etc.) and were caught also in the neighbouring *Combretum-Dalbergia* association, especially where this included *Acacia spirocarpa*. A few were usually captured in the tall *Acacia xanthophloea-A. usambarensis* woodland along the north edge of the block. *G. swynnertoni* was widely distributed and nowhere particularly dense. It was constantly found in the tall acacia woodland, at the boundary of the gall acacia and the *Combretum-Dalbergia*, and on the " Green Path " (*Combretum-Dalbergia* plus *A. spirocarpa*) (see Hocking & others, 1954), as indeed it had been before the first experiment on the area.

Operational Details.

The principles governing the control of tsetse from the air by means of non-persistent insecticides have been discussed in an earlier paper in this series (Hocking & Yeo, 1953) to which reference should be made.

Eight applications of insecticide were planned for the present experiment, to cover the period 23rd January to 5th May at two-weekly intervals. The proposed mean nominal dosage was 0·25 lb. technical BHC (12–13 per cent. γ isomer) per acre per application. The insecticide was dispersed as a coarse aerosol of droplet range 5–250 microns, mass median diameter 70 microns, from a pressurised boom carrying Bray jets and fitted to an Anson Mk. 1 aircraft.

Insecticide and apparatus.

Only one aircraft was available and to obtain the required area dosage it was necessary to use insecticide of twice the usual strength emitted at half the rate used in previous operations carried out by this unit. This was made possible by the use of a BHC concentrate stated to contain 25 per cent. γ isomer, which was dissolved in a mixture of 50 per cent. Shell Diesoline and 50 per cent. Shell Power Kerosene, as used on the Galapo Block. The equivalent of a 20 per cent. technical BHC solution, equivalent to 2·45 per cent. γ isomer, was expected; in fact the strength varied between 17·6 and 22·4 per cent. with a mean of 19·4 per cent. This mixture had a drop spectrum similar to the 10 per cent. DDT solution in the same solvents and was dispensed from the same pressurised boom apparatus (Hocking & others, 1954). The lower emission rate was obtained with fewer jets and this made it possible to remove the outboard section of the spray boom without affecting the swathe width appreciably. This greatly improved the handling of the aircraft and permitted an increase in speed from 100 to about 105 m.p.h.

Personnel and transport.

European staff at Kikore consisted of an entomologist and two field officers. A radio operator came down by road for each application; two-way radio communication reduced the considerable danger of operating in the prevailing conditions. Eight Africans were employed on fly-rounds and carried the portable markers used to indicate to the pilot where to begin his spray run. A number of labourers was constantly employed, principally on roads and buildings.

There was one reliable 30 cwt. truck on the station, one ex-military vehicle and also two private cars, but the roads rapidly became impassable for these.

Spraying procedure.

In order to cover the area with one aircraft, especially when the Kikore bush airstrip became unserviceable and the Anson had to operate from Arusha, the time spent in the air when not actually emitting had to be cut to a minimum. This was assisted by having markers at both ends of the block, moving along each of the roads. The aircraft flew consecutive swathes in opposite directions, alternately due north and south (magnetic), and each marker moved up two swathe-widths between consecutive runs from his own end. The runs were in some parts long, but with experienced pilots the accuracy of tracking was remarkable, although apt to be upset if reference marks on the hills were obscured by low cloud. The presence of a man at the far end made possible a good check on accuracy of coverage as the marker was usually invisible until the last moment and last minute changes of course could not be made. The controller moved with the southern marking party in a truck carrying the radio. This was very successful so long as the road was passable, after which the radio remained at base and the marker was carried on foot. It was found that with the almost invisible aerosol its behaviour could only be judged from close at hand. There was no instrumental check on meteorological conditions, which were judged visually by the rate of dissipation of smoke puffs fired from a Verey pistol.

The daily overlap, based on previous experience, was fixed at 450–500 yards and was increased to 600–650 yd. if a day was missed due to bad weather. The overlap is necessary to kill flies which enter the treated area from the untreated part, between sorties.

Dosage and coverage in practice.

The time spent in actual spraying was reduced to a minimum and the end of each sortie hastened by using the widest possible effective swathe. A trial at Arusha in a very light wind gave an almost constant ground deposit between 80 and 110 yd. downwind and it was decided to use a 90-yd. swathe to start with. Available information indicated that the aerosol penetrated bush satisfactorily but later work has shown that in leafy *miombo* the effective swathe width is considerably reduced compared with that obtained in similar conditions of wind speed, etc., in the open. Fly rounds done after the first application showed the dosage, especially over the western part of the block, to have been inadequate. This was because (a) the emission rate was less than the 4 gals. per min. obtained in trials and (b) the short boom allowed an increase in economical cruising speed, *i.e.*, the speed at which spraying was carried out, by 5–10 m.p.h. This increase in speed was desirable because it made flying safer and reduced the time spent in the air. Also, (c) the swathe width was probably too great, especially over the thicker parts of the bush. The emission rate was increased to an expected 4·3 gal. per min. by adding another jet and the swathe width reduced to 75 yd. over the western half of the block, which included the important areas of the *miombo*. This spacing was used for the second and all subsequent applications.

The actual area dosage varied from one application to another owing to the different proportion of the total flying which was done from Kikore (with increased loads of insecticide and less overlap), and the number of interruptions experienced, which increased the expenditure on overlap. As an example, application seven, done by flying from Arusha, extended over seven days, on five of which flying was possible. The overall mean area dosage was 2·42 lb. technical BHC per acre.

Weather.

All previous experience showed that when operating from Arusha very little emission of insecticide would be possible in first-class meteorological conditions. In practice the sun was usually covered during the time the aircraft was over the block, while applications 3, 5, 6, 7 and 8 (incomplete) were carried out beneath dense low cloud. Thus although little work was done in really bad meteorological conditions these were very seldom excellent (*cf.* Yeo & Thompson, 1954).

TABLE II.

Catches of *Glossina morsitans* and *G. swynnertoni* in the North Block at Kikore.

Date	*G. morsitans*			*G. swynnertoni*		
	North Block		Control (Hillside)*	North Block		Control (South Block)†
	A.D.	Total	A.D.	A.D.	Total	A.D.
25.xi.50	5·3	26	810	2·7	14	2·6
16.xii.	5·3	23	952	4·7	19	7·8
23.xii.	6·0	49	823	2·0	12	
30.xii.	3·9	36		3·6	25	
6.i.51	4·5	35	1058	1·7	15	7·8
13.i.	3·9	36	796	1·4	20	
20.i.	9·0	55	785	2·0	20	
FIRST APPLICATION						
29.i.51	2·3	11		0·3	2	
5.ii.	7·0	21	909	1·3	7	
SECOND APPLICATION						
12.ii.51	0·3	3	777	0·3	1	
29.ii.	2·8	7	1129	0·7	2	7·8
THIRD APPLICATION						
26.ii.51	0·3	1	781	0·7	2	
5.iii.	0·3	3	946	0·3	2	
FOURTH APPLICATION						
10.iii.51	0·3	1	876	0	0	16·7
17.iii.	0·3	3	788	0	1	
FIFTH APPLICATION						
24.iii.51	1·0	3	808	0	0	
1.iv.	0·7	2	720	1	3	
SIXTH APPLICATION						
11.iv.51	0·0	1	798	0	1	8·1
17.iv.	1·3	4	748	0·3	1	
SEVENTH APPLICATION						
26.iv.51	0·0	2	693	0·3	1	
2.v.	1·0	3	724	0	0	
EIGHTH APPLICATION						
7.v.51	0·3	1	752	0	0	
19.v.	1·0	3	559	1·3	4	6·7
26.v.	0·7	3	563	0·3	1	
June 1951	2·3	8	765	0·5	2	7·8
July	5·1	10	645	0·9	4	8·1
Aug.	2·7	9	776	0·8	3	3·7
Sept.	2·4	9	710	0·7	2	1·1
Oct.	2·7	12	656	0·6	2	1·9
Nov.	3·3	13	654	0·3	2	2·4
Dec.	3·2	12	583	0·5	2	1·1
Jan. 1952	2·0	7	627	0·5	1	0·6
Feb.	1·2	7	543	0·9	4	3·0
Mar.	3·0	11	537	1·3	5	3·4
Apr.	1·5	6	596	2·0	7	3·4
May	2·1	8	570	1·2	6	2·8
June	1·7	9	598	1·3	4	3·9
July	0·3	5	599	0	0	2·0
Aug.	2·0	6	396	0	0	—
Sept.	2·0	6	289	0·3	1	—
Oct.	0·7	4	296	0	0	—
Nov.	2·0	6	245	0·2	0·5	—
Jan. 1953	4·0	16	370	2·0	6	—

Between 25th November 1950 and 26th May 1951 the figures are given for individual sets of fly-rounds. From June 1951 onwards mean figures are given for the rounds carried out each calendar month. A.D. = Apparent Density, which is the number of non-teneral males caught per 10,000 yd. of fly-path. For final figures see Note on p. 612.

* Hocking & others (1954).

† Hocking & others (1953).

Throughout the period there were many interruptions to flying due to bad weather at Arusha, or at Kikore, or in between. Interruptions would have been many fewer if the base and operational areas had not been so far apart. Low cloud rather than actual precipitation was the chief nuisance and at times made flying dangerous. In April, rainfall was exceptionally heavy and eventually the experiment was abandoned when flying had been cancelled on three consecutive days after the first day of application 8.

Rainfall and its effect on operations are summarised in Table I.

TABLE I.

Rainfall at Kikore field station and the effect of bad weather on operations over the North Block, Kikore in early 1951.

Month	Jan.	Feb.	Mar.	April	May 1–14th	Total
Rain (inches) ..	4·53	6·21	3·30	23·14	2·89	40·07
Rain (days)	9	17	11	23	12	72
Days flying completed	4	10	7	12	1	34
Days flying cancelled ..	1	3	0	4	3*	11

* Experiment abandoned after cancellation on three successive days.

Results.

Chemical and physical assessments.

Staff was not available to make these on an adequate scale. Apart from the check made at Arusha on the drop spectrum and swathe width mentioned above (p. 607), test papers were laid across two swathes during normal spraying. This was done in the open in the small plain or *mbuga* near the north edge of the block (see map in Hocking, Parr & others, 1953). There was a rather low total recovery but no pronounced gap in the deposit.

Entomological results.

The four fly-rounds laid out before the 1949 trial remained in use throughout the present experiment. The number of tsetse was too small for a satisfactory population estimate to be made by releasing and recapturing marked flies (Jackson, 1948), with the staff and time available. During January 1951 the mean " apparent density " of *G. morsitans* (*i.e.*, the number of old males caught per 10,000 yd. of fly path) was 6·6 and was rising rapidly, being 9·0 for the last set of rounds before treatment started. In June 1949 the number of old male *G. morsitans* in this block was estimated at 8,000 and the mean apparent density was 163 (Hocking & others, 1953). If the populations were in constant ratio to the apparent densities the mean number of old males in January 1951 was 324 (52 per square mile). The relative climatic conditions in the two periods make it likely that this is an over-estimate as they were both dry periods and it was much hotter in January 1951, increasing the activity of the tsetse and bringing a higher proportion of them to the catchers. The number of *G. swynnertoni* in the block had not been estimated previously.

The results of fly-catches made before, during and after the operation are given in Table II. No pupal survey was attempted with such small numbers present. The control used was the same as for the Galapo Block (see Hocking & others, 1954).

The first application gave the following reductions in apparent density and total captures :—

G. morsitans :	Reduction in A.D. 67 per cent. ;	in total catch 80 per cent.
G. swynnertoni :	,, ,, ,, 85 per cent. ;	,, ,, ,, 90 per cent.

Thus, although neither species was reduced to the extent desired, *G. morsitans* was apparently the less affected. Out of 11 specimens of this species caught just after the first application, two had been marked in the attempt to estimate the pre-spraying population. Within a week the apparent density of *G. morsitans* had returned to what it had been before the application, although the total catch did not recover to the same extent (Table II).

The second application at higher dosage was more successful but at no single date was a nil catch recorded. Two old females were taken after the seventh application and it is not likely that the completion of the eighth would have affected the results. The percentage reduction in apparent densities of the males of the two species are given below, together with the natural fall in the controls. To obtain these figures the mean apparent densities for all fly rounds done in January, before the first application, are averaged and compared with similar averages for rounds done in May after the last application was abandoned.

	North Block	Control
Reduction in A.D. of *G. morsitans*	88 per cent.	39 per cent.
Reduction in A.D. of *G. swynnertoni* ..	69 per cent.	14 per cent.

The reduction due to the insecticidal treatment alone has been calculated using Abbott's formula, *i.e.*

$$\text{Mortality due to experimental treatment} = \frac{\text{s.c.}-\text{s.e.}}{\text{s.c.}} \times 100$$

where s.c.,s.e. are the percentage survivals of insects exposed to control and experimental conditions respectively. This adjustment gives :—

Reduction in *G. morsitans* due to insecticidal applications = 80 per cent.
Reduction in *G. swynnertoni* due to insecticidal applications = 64 per cent.

During the dry season of 1951, catches in the block increased despite very cool weather and a further fall in the control. The rise continued slowly until September 1951 (*G. swynnertoni*) and December 1951 (*G. morsitans*). Catches then fell and the normal seasonal rise of the next early dry season was less than in that directly following the experiment. Numbers were generally lower in 1952 than in the previous year. There was a particularly steep fall in catches of *G. morsitans* in both block and control in the late dry season of 1952 (Table II). The control area for *G. swynnertoni* was cleared in August 1952.

Discussion.

This experiment may be compared with both the previous trial on the same block (Hocking & others, 1953) and with that carried out on the Galapo area (Hocking & others, 1954). In the first case the area is in common but the bush was in very different condition of leaf and the insecticide was applied in different forms, in the earlier trial as a thermally-generated aerosol of 10 per cent. DDT and in the present experiment as a coarse aerosol of 20 per cent. BHC dispersed from a boom. The Galapo area was treated with the boom apparatus and 10 per cent. DDT and was in leaf after the third cycle of treatment. It is, however, impossible to make clear comparisons because of various complicating factors. Any increased efficiency of dispersal of insecticide which was shown on the Galapo Block was probably more than discounted in the second North Block experiment by the increase in swathe width and reduction in droplet numbers due to the halved emission rate. The leafiness of the trees is believed to have been the main reason for the lack of final success in the Galapo area and although the small-leaved acacias there were probably more efficient at removing just those drops of a size to impact on a tsetse fly, the larger-leaved but deeper canopy of the *miombo* may have had an equally unfortunate effect in narrowing the effective swathe width. This would be due to reducing the wind speed and offering an extensive vertical surface to the drifting cloud of aerosol. The first application of insecticide to the North Block in 1951 was less efficient against the *G. morsitans* in the *miombo* than against *G. swynnertoni* in the more open acacia and combretaceous areas. By increasing the emission rate over the whole area and reducing the swathe width over the western half alone both species were more efficiently attacked and *G. morsitans* suffered a proportionately greater reduction. It is however impossible to say what might have been the ultimate effect of these measures because the weather prevented them from being applied properly. The rains of the season were some of the heaviest and most prolonged which have been experienced in the area, but except in seasons of drought the same difficulties will always be met with anywhere in East Africa. If the airbase and the area to be sprayed are far apart no insecticide will be expended in really favourable meteorological conditions, and most of the country is remote from all-weather air strips. Actual interruptions mean increased expenditure because overlaps have to be extended for each day on which flying is not done. Overheads are extremely high and it is desirable to employ the aircraft as fully as possible by flying nearly every day. Interruptions to a schedule of this type soon result in one application extending into the next cycle, delaying its start, and resulting in the interval between cycles becoming greater than the minimum period for young tsetse to mature their first larva. This is sufficient by itself to ensure failure to exterminate.

Summary.

The "North Block" at Kikore, Central Province, Tanganyika, was treated with insecticide dispersed from an Anson 1 aircraft during the period 23rd January to 4th May 1951. The area consisted of some 4,000 acres of mixed bush, including about 230 acres of *miombo*, infested by two species of tsetse fly, *Glossina morsitans* Westw. and *G. swynnertoni* Aust.

The insecticide used was equivalent to a 19·4 per cent. solution of technical BHC (equal to 2·45 per cent. γ isomer) in 50 per cent. diesel oil, 50 per cent. power kerosene. The solution was dispensed through a boom and nozzles under pressure as a coarse aerosol (mass median diam. 70 microns), at a nominal mean dose of 0·25 lb. technical BHC per acre per application. Eight applications were planned and seven completed.

The first application was relatively ineffective, and for the second and subsequent cycles the emission rate was increased and over part of the block the swathe width was reduced. The result was a much improved kill but neither species of tsetse was exterminated.

Owing to the number of factors involved, it is not possible to give any principal reason why this experiment was less successful than previous ones, but many of the difficulties encountered are inherent in rainy-season operations in East Africa.

Acknowledgements.

We gratefully acknowledge the assistance given by other members of the Colonial Insecticide Research Unit in this operation; to Mr. D. Yeo and Messrs. E. T. Mesmer and H. V. Newton who carried out the physical and chemical assessments, respectively, and to Mr. S. Znatowicz who did much of

the field work. The aircraft was operated and flown by the staff of Messrs. Airwork Ltd., London.

The work has been financed by the Colonial Development & Welfare Funds and directed by the Colonial Insecticides, Herbicides and Fungicides Committee.

References.

Hocking, K. S. & Yeo, D. (1953). Aircraft applications of insecticides in East Africa. I.—Bull. ent. Res., **44**, pp. 589–600.

Hocking, K. S., Parr, H. C. M., Yeo, D. & Anstey, D. (1953). Aircraft applications of insecticides in East Africa. IV.—Bull. ent. Res., **44**, pp. 627–640.

Hocking, K. S., Yeo, D. & Anstey, D. G. (1954). Aircraft applications of insecticides in East Africa. VI.—Bull. ent. Res., **45**, pp. 585–603.

Jackson, C. H. N. (1948). The analysis of a tsetse-fly population. III.—Ann. Eugen., Lond., **14**, pp. 91–108.

Yeo, D. & Thompson, B. W. (1954). Aircraft applications of insecticides in East Africa. V.—Bull. ent. Res., **45**, pp. 79–92.

NOTE.

It has been learnt that this block is to be cut down in June 1954 as part of a reclamation scheme. The following figures bring Table II up to date and conclude the following up of this experiment. There has been no control for *G. swynnertoni* since the South Block was cut down in August 1952. The increase in *G. morsitans* is attributed to various factors favouring immigration from the nearby hillside across the (largely regenerated) barrier clearing.

Date	*G. morsitans*			*G. swynnertoni*	
	North Block		Control	North Block	
	A.D.	Total	A.D.	A.D.	Total
Feb. 1953	3·0	9	427	0·7	2
Mar.	1·7	7	364	1·0	4
Apr.	2·0	8	353	0·7	3
May	2·3	8	404	1·7	5
June	3·3	11	485	1·3	4
July	4·7	17	534	1·0	3
Aug.	5·3	17	478	1·7	5
Sept.	4·3	17	422	2·0	7
Oct.	6·0	21	425	3·0	9
Nov.	6·7	24	428	3·3	10
Dec.	3·9	16	472	1·6	4·3
Jan. 1954	4·6	19	497	1·5	4·8
Feb.	6·3	23	444	1·1	4·8
Mar.	6·3	33	426	1·1	3·7
Apr.	8·2	34	434	0·6	2·1
May	10·8	38	438	0·6	2·0

A.D. = Apparent Density.

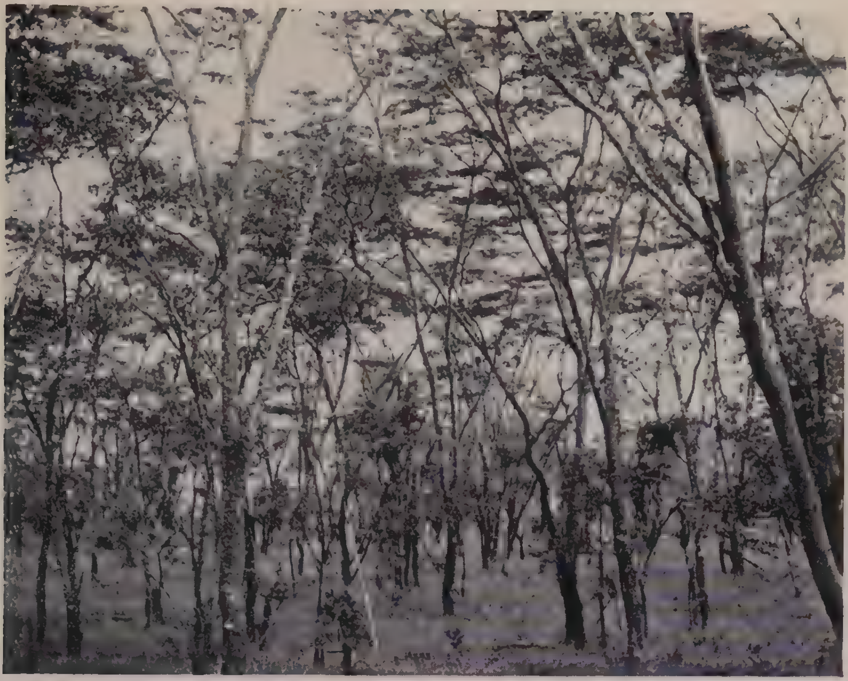


FIG. 1. Miombo woodland. Principally *Isoberlinia globiflora* with some *Brachystegia microphylla*. The main habitat of *G. morsitans* in this block.

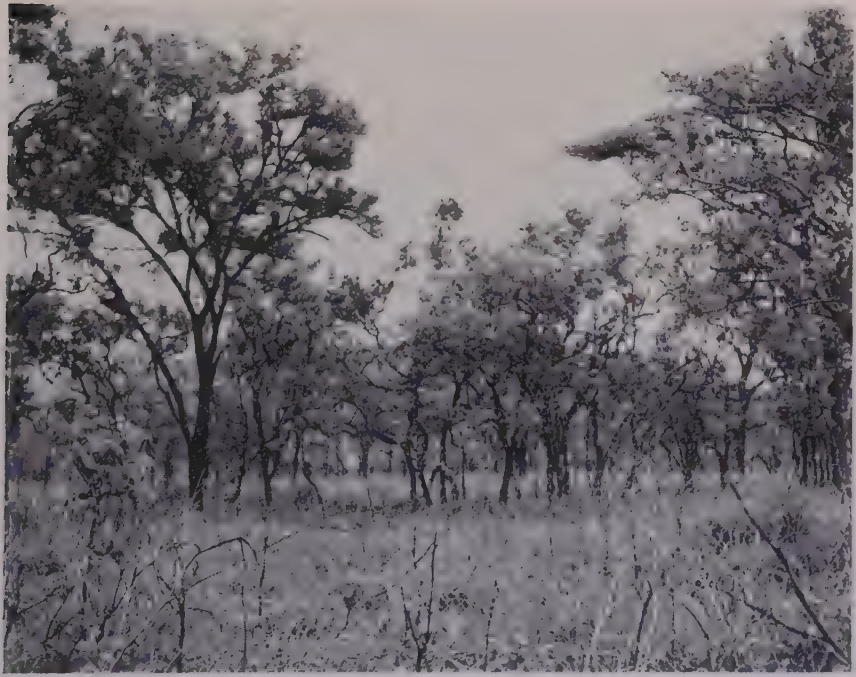


FIG. 2. Combretaceous woodland with *Acacia spirocarpa*, supporting both *G. morsitans* and *G. swynnertoni*.

VEGETATION IN THE NORTH BLOCK, KIKORE, AT THE START OF THE MAIN RAINS. TREES IN FULL LEAF BUT GRASS STILL SHORT.

AIRCRAFT APPLICATIONS OF INSECTICIDES IN EAST AFRICA. VIII.—AN EXPERIMENT AGAINST THE TSETSE FLY, *GLOSSINA SWYNNERTONI* AUST., IN AN ISOLATED AREA OF THORNBUSH AND THICKET.

By K. S. Hocking, G. F. Burnett and R. C. Sell.
Colonial Insecticide Research Unit, Arusha, Tanganyika.

(Plate XLII.)

Previous applications of insecticide by aircraft against savannah tsetse flies have reduced the apparent density of these insects to zero, often for several weeks, but small numbers of fly have subsequently appeared in the area treated (Hocking, Parr, Yeo & Anstey, 1953; Hocking, Yeo & Anstey, 1954). Although the blocks of bush concerned were surrounded by barrier clearings which were considered on available information reasonably fly-proof, and which could not have been increased in width except at undue expense, it was possible that immigration was the reason for the reappearance of the tsetse.

There are a number of comparatively cheap methods by which tsetse may be more or less permanently reduced to low densities but, if lasting results are to be obtained by insecticidal methods alone, complete elimination is necessary. The use of an expensive method such as aircraft applications of insecticide is likely to be justified in normal circumstances only if complete extermination can be achieved. Before proceeding further it was necessary to carry out an experiment in an area where possible immigration would not be a complication. The initial numbers of fly were not so important and, if necessary, additional measures, such as extra applications or ground attack on persistent foci, would have been used to obtain elimination.

A suitable and convenient site was thought to be Atta " island " near Kikore (approx. Lat. 04°35′S., Long. 35°51′E.) in the Central Province of Tanganyika. This had been isolated by the East African Tsetse and Trypanosomiasis Research and Reclamation Organisation (E.A.T.T.R.R.O.) for an experiment with BHC smoke generators (J. H. Crawford, unpublished, 1950). This experiment reduced the apparent density of old males (exclusively *Glossina swynnertoni* Aust.), as given by standard fly rounds, from 23·2 to about 0·5 per 10,000 yards, but did not eliminate the tsetse. Numbers slowly increased after this experiment but the increase did not continue indefinitely and for the year before the present experiment catches had been more or less constant. The failure to increase further may have been due to the great reduction in *G. swynnertoni* in the nearest area of infested bush when it was treated from the air by this unit between July and November 1949 (Hocking, Parr, Yeo & Anstey, 1953). This would imply that failure to increase was due to absence of immigration from elsewhere on a measurable scale.

Description of Area.

Atta is about two miles south of the original " South Block " at Kikore (Hocking & others, 1953) and its nearest point is twelve miles from the field station and about five miles from the airfield. It is a well-marked area of thornbush and thicket about $3\frac{1}{2} \times 1\frac{1}{4}$ miles in extent (see fig. 1 & Pl. XLII, figs. 1 & 2) on an area raised distinctly above the surrounding *mbuga* (*i.e.*, open grassland subject to seasonal flooding and waterlogging). In the past it was " surrounded by gall acacia and joined to the Kisese fly-bush to the north [*i.e.*, the " South Block "], the Itororo bush to the west and by small isolated patches of fly-bush to the large *G. morsitans–G. swynnertoni* block in the south." (Crawford, *loc. cit.*). The isolation of the block was completed by E.A.T.T.R.R.O. and nowhere were the clearings less than 1½ miles wide, wider than they have been in some places around the blocks previously treated from the air. For most of December and early January and in February the *mbuga* was flooded and Atta was literally an island.

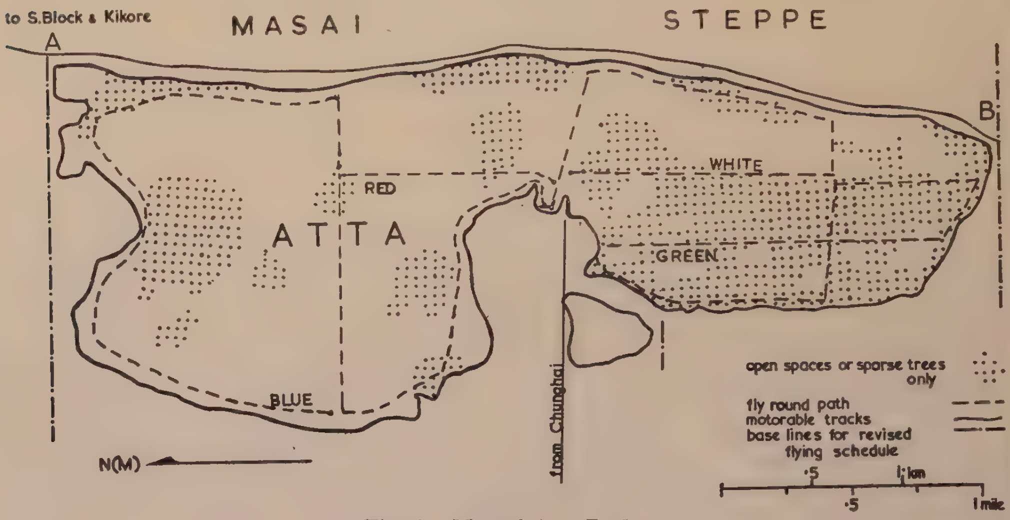


Fig. 1.—Map of Atta Bush.

Vegetation.

The vegetation is all of one type but patchy and the bush includes small *mbuga* and hard-pans. There is no continuous high canopy but much *Commiphora fischeri* thicket interspersed with tall *Acacia spirocarpa* and baobabs (*Adansonia digitata*) and shorter species, notably *Acacia mellifera*, *A. kirkii*, and *Albizzia sericocephala*. Of the tall trees, *A. spirocarpa* is by far the most abundant. Even where densest they are spaced out from 50 to 300 yards apart, often occurring in groups. Thickets include, in addition to *C. fischeri*, another *Commiphora*, *Acacia pennata*, *Fagara chalybea*, *Dichrostachys glomerata*, *Grewia bicolor*, *Terminalia stuhlmannii*, *Maerua* sp., *Rhus incana*, etc. The edge of the hard-pans support *Albizzia anthelmintica*, and *Acacia drepanolobium*. The slope along the eastern boundary is covered in many places with *Lannea humilis* sometimes so dense as to be thicket-like, and below this and also round most of the edge is a broken belt of gall acacia, principally *A. formicarum*. Grass growth is not very dense or tall. Each year the area is swept by fires.

During the whole of the experiment there was a considerable amount of foliage on the trees; the thickets came into leaf as the experiment progressed (Pl. XLII, figs. 1 & 2).

Game animals.

Game was not abundant but fly-boys on their rounds reported Coke's hartebeest, ostrich, giraffe, impala, rhinoceros, wart-hog, eland and roan antelope.

Distribution of fly.

Crawford (*loc. cit.*) reported no *Glossina morsitans* Westw. in Atta, but four specimens were caught in three sets of pre-treatment rounds. *G. swynnertoni* was the only species present in important numbers. It was nowhere particularly abundant before spraying but in particular very few were caught in the southern tip. They were most common along the eastern edge and some were regularly captured in the north-east corner (Blue Path—see map) and along the north edge of the bay on the western side (Red Path).

There were too few tsetse present for an attempt to estimate their numbers by marking (Jackson, 1948) but an estimate was made at this time of a population of *G. swynnertoni* in the course of other work in an area twenty miles away (Burnett, 1954). If the proportion captured on standard fly-rounds was the same in both cases the true density of non-teneral males in Atta was about 70 per square mile, with probably twice that number of females present in addition.

Operational Details.

The principles governing the control of tsetse from the air by means of non-persistent insecticides have been discussed in an earlier paper in this series to which reference should be made (Hocking & Yeo, 1953). Eight applications of insecticide were planned with a fourteen-day interval between the commencement of successive applications. It was not possible to start before the first week in November 1951, as preliminary fly-rounds had to be done. With normal weather there would have been time for eight applications before the onset of the long rains in late March. The aircraft was based on the Kikore airstrip and it was intended to fly from Arusha, 90 miles away, if Kikore became unserviceable during the short rains. In a normal season only one or at most two applications would be expected to be affected.

Insecticide and equipment.

The insecticide used was a 10 per cent. w/v solution of technical DDT in 50 per cent. Shell Power Kerosene/50 per cent. Shell Diesoline. It was applied at a nominal dosage of 0·25 Imp. gals. per acre per application. The dispensing apparatus was that described by Hocking, Yeo & Anstey (1954) but was modified by mounting the jets closer together on the centre section of the boom and dismounting the outboard sections. This had no adverse effect on the swathe width or drop-spectrum, but greatly improved the handling of the aircraft and increased the airspeed by 5 to 10 m.p.h. The apparatus produced a coarse aerosol of mean volume diameter 70 microns and drop range 5 to 250 microns. The emission rate was 10 gals. per minute. Only one aircraft (Anson Mk. 1) was available for this experiment.

Field methods.

The swathe width throughout the experiment was 88 yards. With a narrower swathe and lower emission rate each day's flying would have extended into the period of unfavourable meteorological conditions. Reduction of the swathe width would therefore have led to a reduction in the daily coverage and a single aircraft would not have been able to carry out the operation.

The first three applications were made by flying across the block on its smallest dimension, due east to west (magnetic). The marker moved along the road which runs along the eastern edge of the area, starting from the north (A to B on map, fig. 1). During the third application, assessments showed that coverage was possibly inadequate, the prevailing wind in the early morning being so easterly that the aerosol cloud was not adequately covering the wide swathe. Accordingly a rather complex flying schedule was made out which involved making timed runs from a base line off each end of the block, finishing each run at the narrowest part (see map, fig. 1). It was only the presence of the bay on the western side, which was assumed to be a sufficiently fly-proof barrier, that made this procedure possible. It was, however, necessary to fly the first day's sortie from the southern end of Atta. Thus the last part to be covered during the fourth spraying cycle would be the part first sprayed during the third application, *i.e.*, there would have to be an interval of 19 days between the two applications. This period would result in a negligible number of larvae being dropped by young flies which had emerged since the previous application but allowed of little further extension due to bad weather, etc. When unseasonable rain in December made it likely that flying from the advanced airstrip at Kikore would be interrupted an alternative schedule was made out for continuing operations from Arusha. This required an extra day's flying and was of course less efficient because flying to the target occupied the period when the best meteorological conditions for spraying existed.

Staff and transport.

These were representative of what would be used in a practical scale rather than what are usual for experimental work. At Kikore one field officer was engaged on this and other work as well, as were a dozen African fly-boys. Another European officer mixed insecticide and filled the aircraft. Most of the time one vehicle only was available for all the work of the station, another coming down to serve the aircraft and crew. Visits were made during the actual spraying periods by scientific staff from Arusha.

Course of operations.

The first application started on 6th November 1951 and the last finished on 2nd March 1952. Table I shows the serious effect of the unseasonable bad

TABLE I.

The course of operations over Atta. November 1951–March 1952.

Application	Date scheduled to start	Date started	Duration of application in days	Intervals between commencing successive applications	Aircraft based at	Remarks
1	Nov. 6	Nov. 6	4	—	Kikore	
2	Nov. 20	Nov. 20	4	14	Kikore	
3	Dec. 4	Dec. 4	4	14	Kikore	
4	Dec. 18	Dec. 26	10	22	Arusha	Delay in starting and excessive duration due to bad weather
5	Jan. 1	Jan. 10	8	15	Arusha	Duration due to bad weather
6	Jan. 13	Jan. 25	5	15	Kikore	
7	Jan. 29	Feb. 8	3	14	Kikore	Abandoned when aircraft marooned by flooding of air-strip
8	Feb. 18	Feb. 25	7	17	Arusha	Delay due to marooning of aircraft at Kikore. Block covered in reverse of usual order to cover the unsprayed area as soon as possible

weather on operations (*cf.* Hocking, Burnett & Sell, 1954). When the condition of the Kikore airstrip made it necessary to fly from Arusha, many days were lost owing to low cloud and fog which prevented take-off. The most serious delay was in starting the fourth application; it was the first for which the revised flying schedule was in force and this made the delay all the more serious (see above). The interruption to application 7 and the subsequent delay in starting number 8 were due to a violent and local storm which flooded and waterlogged the Kikore airstrip on the night of 10th February when the aircraft was parked there.

TABLE II.

Monthly rainfall at Kikore field station for the wet season 1951–1952.

Month	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	Total
Rainy days	1	11	22	11	10	16	16	14	1	102
Rain (inches).. ..	0·19	3·34	11·03	4·88	10·80	4·23	6·83	4·24	0·6	45·6

Results.

Physical and chemical assessments; Meteorology.

The insecticide was the same as used on the Galapo Block and the apparatus was identical except for the shortened boom. Assessments were needed only to check on the adequacy of the proposed swathe width which was greater than used at Galapo. However this, and the greater airspeed, were more than compensated for by the increased emission rate. As a result of assessments done on the third application, the direction of flight was changed 90° (see above) but the swathe width of 88 yards had to be kept for operational reasons. Subsequent coverage, however, seems to have been adequate.

Meteorological observations were not made for every sortie and there were many interruptions due to rain and low cloud. Conditions of strong inversion were rare and, for the first half of the experiment at least, weak inversions changing to isothermal conditions predominated. When operating from Arusha (applications 4, 5 and 8, Table I) the best conditions were wasted during the flight from base, but the cool cloudy weather of these periods delayed the onset of very bad turbulence. Meteorological conditions may be summed up as being highly typical for aerial spraying in this area during the rainy season.

Table II gives the monthly rainfall at the field station about 14 miles away.

Entomological results.

The four fly-paths, of total length 23,000 yd., which had been used by E.A.T.T.R.R.O. were reopened before the start of the experiment and weekly rounds commenced. Between spraying, rounds were done approximately three days and ten days after each application. There was a gap in the rounds in December due to bad weather and flooding.

Table III summarises the catches made in Atta and the nearby South Block, which was used as a control.

It will be seen that for six months (January to June 1952) no *G. swynnertoni* was caught in Atta. During this period the fly-rounds were done nineteen times, a total of over 250 miles. A number of rounds were done with two bait oxen, as it was thought possible that such a procedure might reveal the occasional fly that did not come to human bait. The period covered the usual seasonal rise in tsetse catches in the early dry season. *G. morsitans* disappeared completely after the first application of aerosol.

The catch of *G. swynnertoni* in the control area fell in December and in February and the average density of non-teneral males, the standard by which tsetse populations are usually compared, fell to nil early in the latter month. This was probably due to the almost complete flooding of this area. Atta is raised above the surrounding plain and the flooding and its effect would be much less marked.

Since the first *G. swynnertoni* was caught in Atta on 10th July 1952, four months after the end of the spraying, other specimens have been caught. Of the eleven captured to the end of March 1953 none has been found in the

TABLE III.

Catches of *G. swynnertoni* on standard fly-rounds in Atta and the control area (South Block, Kikore) before, during and after the aerial spraying of Atta.

Period	Atta		Control	
	Total catch	Av. Apparent Density of old males (per 10,000 yd.)	Total catch	A.D. of old males
Week ending				
20.x.51 ..	15	4·5	7	1·9
27.x.51 ..	17	2·9		
3.xi.51 ..	14	5·7	10	2·6
FIRST APPLICATION				
10.xi.51 ..	2	0·8		
17.xi.51 ..	1	0	6	2·2
SECOND APPLICATION				
24.xi.51 ..	0	0		
1.xii.51 ..	1	0	4	1·5
THIRD APPLICATION				
8.xii.51 ..	0	0		
15.xii.51 ..			3	0·7
FOURTH APPLICATION (interrupted by rain)				
29.xii.51 ..			7	0·7
FIFTH APPLICATION (interrupted by rain)				
12.i.52 ..	1	0		
19.i.52 ..	0	0	6	0·4
26.i.52 ..	0	0		
SIXTH APPLICATION				
2.ii.52 ..	0	0	2	0
SEVENTH APPLICATION (abandoned after 3 days)				
9.ii.52 ..	0	0		
16.ii.52 ..			14	2·7
21.ii.52 ..	0	0	13	3·3
EIGHTH APPLICATION				
March 1952 ..	0	0	12	3·4
April ..	0	0	11	3·4
May ..	0	0	9	2·8
June ..	0	0	13	2·9
July ..	0·5	0·1	7	2·0
Aug. ..	0	0	Block felled in clearing operations	
Sept. ..	0·75	0·1		
Oct. ..	1·0	0		
Nov. ..	0	0		
Jan. 1953 ..	1·0	0·4		
Feb. ..	2	0·9		
March ..	0	0		

Until the end of the spraying the figures are given for individual sets of rounds. After this they are given as monthly means. For final figures see Note on p. 622.

southern part of the area. Except for one female on the northern part of the White Path they have all been captured on the Blue and Red Paths. Before the first was caught, the Kondoa District development scheme had started, accompanied by considerable movement of vehicles, men and cattle. Numbers of poles were cut in Atta and well-sinking took place not far from the block. A tsetse was captured by fly-boys from a car about to pass along the side of the block and it is therefore not possible to be certain whether the flies caught in July (a non-teneral male and female) were carried in or whether the insects persisted undetected within the block.

Discussion.

There were no tsetse caught in Atta until four and a half months after the end of the operation. This is a much longer period than in any similar experiment carried out by this unit, but before comparing the Atta experiment with others it is necessary to ascertain whether this difference indicates a greater proportionate reduction in the fly, or is merely due to missing by chance the survivors of a small initial population reduced only to the same extent as the larger numbers attacked previously.

The percentage reduction obtained in an experiment can be calculated simply on the mean average densities before and after the operation. The post-treatment population is best taken as that during the second month after the end, when all pupae in the ground will have produced adults. In practice the numbers caught are usually so small that it is better to take the mean over the second and third months as the few young flies of the next generation which may appear in this period merely replace the old flies which die. It is also probably better to compare total catches rather than old males alone, for these commonly form a smaller proportion than is usual of the post-treatment catch. In the case of Atta, no flies at all were caught until the fifth month and the post-treatment catch has been taken as the mean for the second to sixth month after the last treatment. This weights any comparison against the Atta operation since the catch includes flies which may have been carried into the " island " from outside, but it does not include their offspring.

The catch actually made in Atta in the second to sixth months, inclusive, has been compared with what it would have been if the percentage reduction had been the same as that attained in *G. swynnertoni* in two earlier experiments.

Actual catch in Atta, months 2–6 after end of experiment	2
Expected catch on basis of reduction achieved in Galapo expt. (Hocking, Yeo & Anstey, 1954)	18
Difference highly significant, P less than ·001	
Expected catch on basis of reduction achieved in North Block (1949) expt. (Hocking, Parr, Yeo & Anstey, 1953)	5
Difference from actual catch not significant, P over 0·2	
Expected catch if compared with North Block catch over months 2–6 instead of 2–3	15
Difference from actual catch highly significant, P slightly over ·001	

Thus there was a genuinely greater reduction in *G. swynnertoni* in Atta than in Galapo but whether the same applies to the North Block is doubtful. The change in significance given above is due to the rapid increase in catches in the North Block as time went on. Immigration was proved to have taken place in the case of *G. morsitans*, which increased at about the same rate, but it is not so likely in the case of *G. swynnertoni* owing to the greater distance involved and the very much smaller number available (about one-fifteenth). The increase can be accounted for theoretically by the natural increment of the residual population, provided circumstances were favourable and the average densities do not represent a smaller proportion of the actual population at the end of the period than at the beginning.

That there may have been no great difference in the results obtained on the North Block and Atta is not surprising. Although the first three applications to Atta were probably done in better meteorological conditions than the whole of the North Block experiment, for which the aircraft flew from Arusha, the operation later suffered many interruptions whereas the earlier trial had none. The bush in Atta bore some leaves at the start of the experiment and became fully leaved later but the leafless bush in the North Block was considerably denser. Although the rate of emission over the North Block was not constant and the mean area dosage therefore varied somewhat this was counterbalanced by the greater swathe width used on Atta, which would also increase the variation in dosage. The small initial population in Atta was probably an advantage since when a small population is reduced to the same extent as a large one the numbers remaining may be too small to meet and breed in the one case, but not in the other.

Why the attack on the Galapo Block should be relatively so unsuccessful is not so plain. Although the bush in the principal habitat of *G. swynnertoni* in Galapo is not much denser than in Atta and although it came into leaf after the third application, the trees in Atta were in leaf throughout. Although the area dosage was about the same in the two experiments, a narrower swathe width was used on the Galapo area, which should be more efficient, and this experiment was carried out throughout in what were probably better meteorological conditions than was the Atta experiment, even when it was possible in that operation to fly from Kikore. For the first three applications to Atta the direction of flight may have led to poor coverage (although in the event it seems that this factor may have been exaggerated), but, most important of all, the operation suffered interruptions which previous experience suggested would be disastrous. Thus all the advantages except the small original population seem to have been on the side of the less successful experiment and unless there was some unknown factor which enhanced the efficiency of the treatment, the small numbers were the deciding factor. Presumably the point was reached at which it was very difficult for the survivors to meet and breed and it appears likely that this point was reached by the end of the third spraying cycle. If this was not so the long interval between the third and fourth applications would have permitted the survivors plus newly emerged flies to produce sufficient pupae to prevent ultimate success. The later applications were all badly affected by weather but seem to have been good enough to kill off sufficient of the young flies which emerged at this time to prevent recovery in numbers.

That a low population level by itself does not ensure success is shown by the second North Block experiment (Hocking, Burnett & Sell, 1954). Here the initial density of *G. morsitans* was about the same as, and of *G. swynnertoni* less than half, that of *G. swynnertoni* in Atta. Neither species was eliminated in an experiment which suffered many interruptions but in which no single application was as effective as the early cycles over Atta. Also, the bush was in many places dense and in abundant leaf and owing to the use of concentrated insecticide at a lower emission rate the number of droplets available to contact tsetse was halved, although the area dosage was the same.

Conclusions.

The reduction of *G. swynnertoni* in Atta was certainly greater than that obtained in the Galapo Block about a year previously. The most likely reason for this is thought to be the smaller initial population in Atta.

Whether the reduction in Atta was greater than in the North Block in 1949 is doubtful, but possible. In this case the small population may be the reason why there was no post-treatment increase of numbers in Atta comparable to that which took place in the North Block.

It is not possible to say whether the tsetse caught in Atta since the end of the experiment are survivors of the original population or whether they or their ancestors were immigrants. It is known that a vehicle carried tsetse to within a short distance of the block and at least one *G. swynnertoni* was caught off it.

Summary.

An isolated area of 2,200 acres of thicket and thornbush in the Central Province, Tanganyika, was treated from the air with a DDT-in-oil aerosol in an attempt to eliminate the tsetse fly, *Glossina swynnertoni* Aust. Eight applications of 0·25 lb. technical DDT per acre were planned to be done at fortnightly intervals. Delays due to unseasonal bad weather reduced this to seven at a slightly higher rate and over a longer period. /ble

G. swynnertoni was reduced from an apparent density of about 7 to zero at the end of the second application. No flies were caught after the fifth application for a period of six months.

It is not possible to say whether the few caught since then have been brought in or are the offspring of survivors of the insecticidal treatment.

This experiment was more successful than that on the Galapo Block in the same area, to a highly significant degree, and this is attributed to the vulnerability of the smaller population present. It was doubtfully better than the first treatment of the North Block, also in this area, because the increase in population in the latter block may have been assisted by immigration.

Acknowledgements.

We are indebted to other members of this unit for their assistance; to Mr. S. Znatowicz who carried out field work in very unpleasant conditions and to Messrs. B. W. Thompson, Meteorologist, and D. Yeo, Physicist, for assessments and advice. The Director and officers of the East African Tsetse and Trypanosomiasis Research and Reclamation Organisation gave us information on the area. An excellent aerial mosaic was prepared by Mr. R. Alken of Messrs. Airwork Ltd., whose staff operated and flew the aircraft.

The experiment was financed from Colonial Development and Welfare funds under the direction of the Colonial Insecticides, Herbicides and Fungicides Committee.

References.

Burnett, G. F. (1954). The effect of poison bait cattle on populations of *G. morsitans* and *G. swynnertoni*.—Bull. ent. Res., **45**, pp. 411–421.

Hocking, K. S., Burnett, G. F. & Sell, R. C. (1954). Aircraft applications of insecticides in East Africa. VII.—Bull. ent. Res., **45**, pp. 605–612.

Hocking, K. S., Parr, H. C. M., Yeo, D. & Anstey, D. (1953). Aircraft applications of insecticides in East Africa. IV.—Bull. ent. Res., **44**, pp. 627–640.

Hocking, K. S. & Yeo, D. (1953). Aircraft applications of insecticides in East Africa. I.—Bull. ent. Res., **44**, pp. 589–600. 41 211

Hocking, K. S., Yeo, D. & Anstey, D. G. (1954). Aircraft applications of insecticides in East Africa. VI.—Bull. ent. Res., **45**, pp. 585–603.

Jackson, C. H. N. (1948). The analysis of a tsetse-fly population. III.—Ann. Eugen., Lond., **14**, pp. 91–108.

Jackson, C. H. N. (1949). The biology of tsetse flies.—Biol. Rev., **24**, pp. 174–199.

NOTE.

It has been learnt that Atta is due for partial destruction as part of a reclamation scheme starting in June 1954. The following figures bring Table III up to date and conclude the following up of this experiment. There has been no control since the South Block was cut down in August 1952 but the catches of *G. swynnertoni* may be compared with those in the North Block (Hocking, Burnett & Sell, 1954).

Atta

	Total catch	A.D. of old males
April 1953 ..	2	0·9
May ..	2	0·9
June ..	2	0·9
July ..	1	0·4
Aug. ..	2	0·9
Sept. ..	2	0·9
Oct. ..	5	2·2
Nov. ..	2	0·9
Dec. ..	2	0·4
Jan. 1954 ..	1·7	0·4
Feb. ..	2·5	0·9
March ..	2·0	0·9
April ..	6	1·3
May ..	3	0·4

A.D. = Apparent Density.

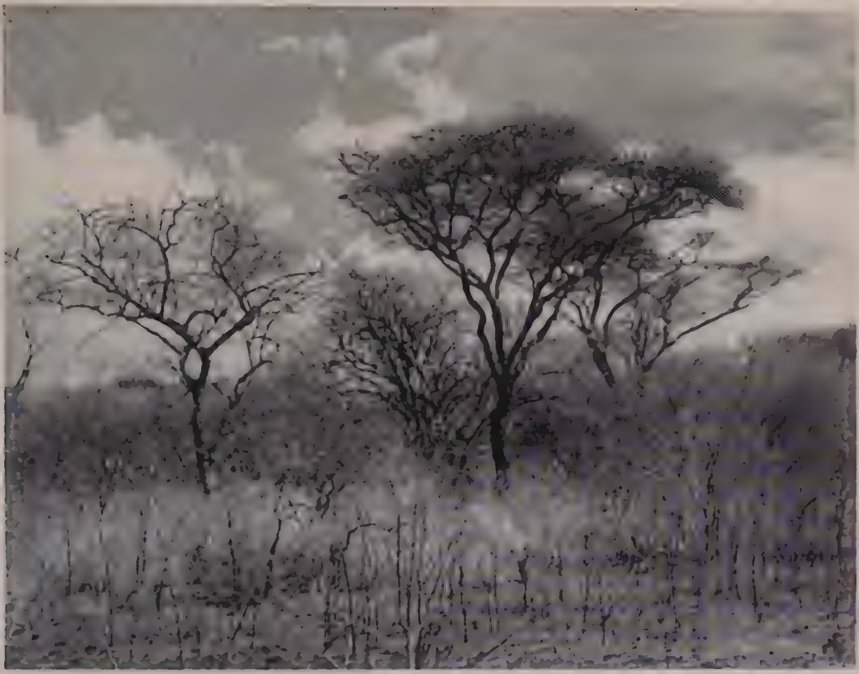


FIG. 1. Atta at the start of the experiment. The *Acacia spirocarpa* on the right has leaves but the *Commiphora fischeri* on the left and the thicket in the background are still leafless.

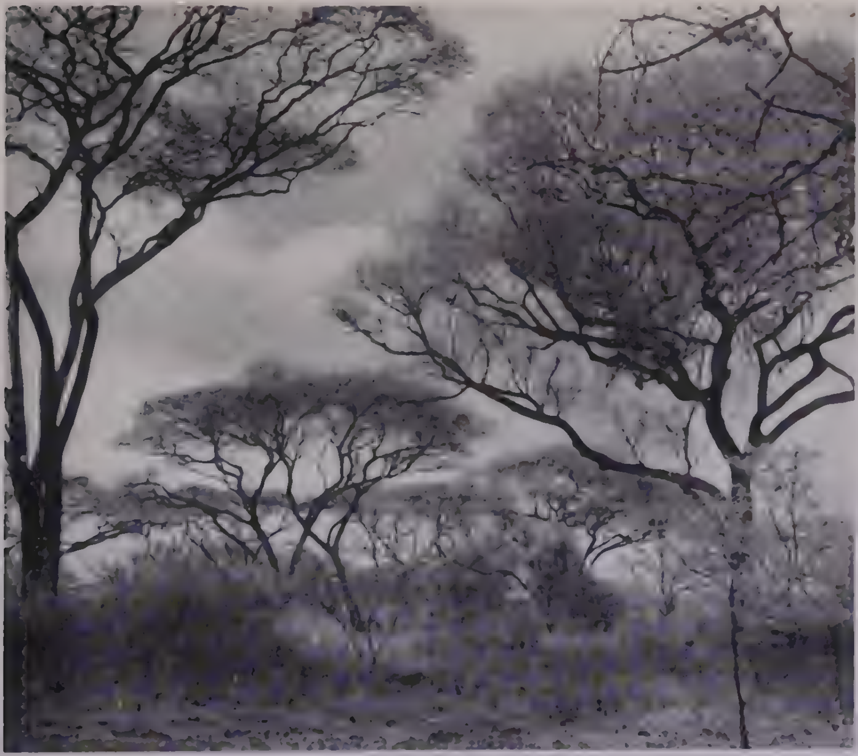


FIG. 2. The bush in leaf in an area where *Acacia spirocarpa* was fairly frequent. The undergrowth in most of the area was considerably thicker and taller than at this point.

FRUIT TREE APHIDS OF ISRAEL.

By E. Swirski. E.M.N.
Agricultural Research Station, Rehovot.

The study of the life-histories of Aphids as outlined in this paper, was approached by three methods: (a) survey of the composition and size of populations, (b) field and laboratory experiments, and (c) extensive observations on a large number of hosts.

Hyalopterus pruni (Geoff.).

Host-plants: Primary.—Almond, apricot, peach; Secondary.—Common reed (*Phragmites communis*), and bulrush (*Arundo donax*).

Life-History.

Bodenheimer (1935) found this Aphid during the period from April to June both on fruit trees and on reeds, and on the latter also in July. On the basis of his own and Hall's (1926) observations in Egypt, Bodenheimer concluded that in the eastern Mediterranean area the Aphids can live at the same time on both types of host. Plaut (1949) recorded infestations on almond trees from March until August. The fate of the Aphids in autumn and winter, the time and form of invasion of the fruit trees, and the relation between the populations on the two categories of hosts remained obscure.

Monthly observations and counts were made in Wadi Rubin (coastal plain) from June 1949 to May 1950. Parallel investigations were carried out in Ein-Harod (Esdraelon valley) and in the Tel-Aviv area. It was found that reproduction is parthenogenetic throughout the year on common reed.

Observations, studies on the composition of populations and experiments to be described below, have shown that *Hyalopterus pruni* attacks almond trees in the autumn and continues its development on them in a sexual cycle. Hatching of overwintering eggs takes place in the coastal plain during the second half of February and in the eastern Esdraelon valley at the beginning of February. Following a period of parthenogenetic breeding, *migrantes* appear in April and May and move on to the common reed. Small colonies of wingless forms remain on almond and then gradually disappear in the course of the summer.

Apricots are similarly infested in autumn, but the existence of a population in the spring depends, among other factors, on the presence of flowers and leaves at the time of egg-hatching. Thus a severe infestation occurred at Miqve-Israel (coastal plain) in autumn 1950, but there was no evidence of it in the following spring, the young larvae having died of starvation as the buds were still closed at the time of hatching.

The only occasion on which peach trees were found to be attacked was in May 1951 when a heavy infestation was seen in the Huleh valley.

Fluctuations in Population.

On common reed.

Fourteen groups of plants growing under different conditions were selected in Wadi Rubin and 100 plants of each group (1,400 in all) were examined monthly. The following records were taken: the number of affected plants; the number of aphid colonies on these plants; the size of the colonies, classified according to the number of Aphids per colony, (a) 1–5, (b) 6–25, (c) 26–40, (d) 41–100. Averages of 3, 15, 30, and 70 were assumed for the various classes, respectively. Thus a rough estimate of the number of Aphids per 1,400 plants could be arrived at. The number of Aphids on plants completely covered by the pest was estimated by counting the Aphids covering a given leaf area and measuring the area concerned on ten plants. The average number of Aphids per sq. cm. was found to be 58, while the total area of ten plants amounted to 5,450 sq. cm. In this way the average number of Aphids on a solidly infested reed plant was calculated as $545 \times 58 = 31{,}610$.

There are two annual peaks in the size of the population, the major one at the end of spring and another one in autumn (figs. 1, 2). In summer and winter, and especially during the latter season, the population is at a low level.

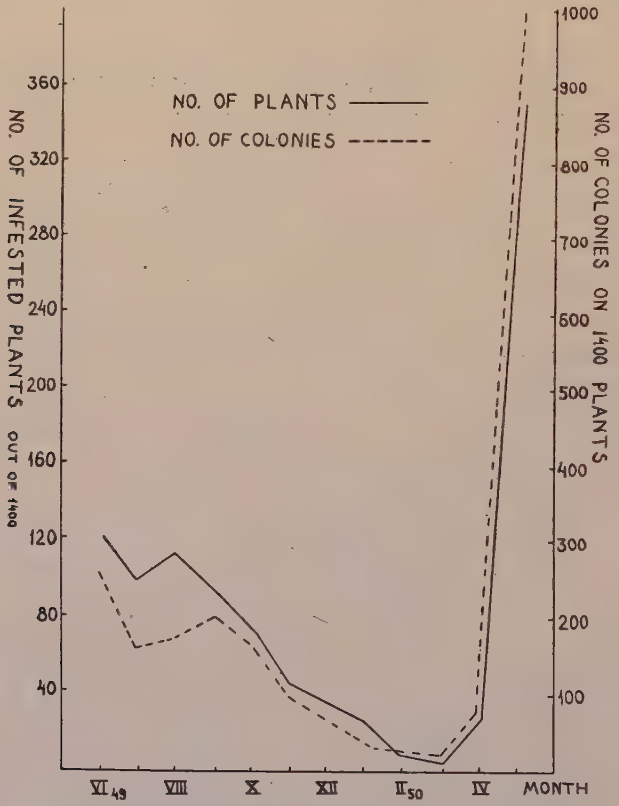


Fig. 1.—Fluctuations in population of *Hyalopterus pruni* on common reed at Wadi Rubin.

Composition of the population.—Alate forms were in evidence during the whole year, with the exception of February, and their proportion in the total population was highest in April. According to Smith (1936), the winged forms developing on reeds do not reproduce on these plants, but migrate to fruit trees for this purpose. The presence of reproducing *alatae* on the reeds at Wadi Rubin could not be considered conclusive, however, owing to the possibility that development might have been accomplished on fruit trees. In an experiment conducted in Tel-Aviv in May 1950, all the Aphids other than larvae of *alatae* were removed from 30 leaves of common reed, while the larvae, numbering 150, were enclosed in bags. A fortnight later large populations were found in twenty bags. The larvae had turned into alate viviparous females which bred on this host. This observation confirms the existence of an alate form which migrates from one reed plant to another, establishing new colonies.

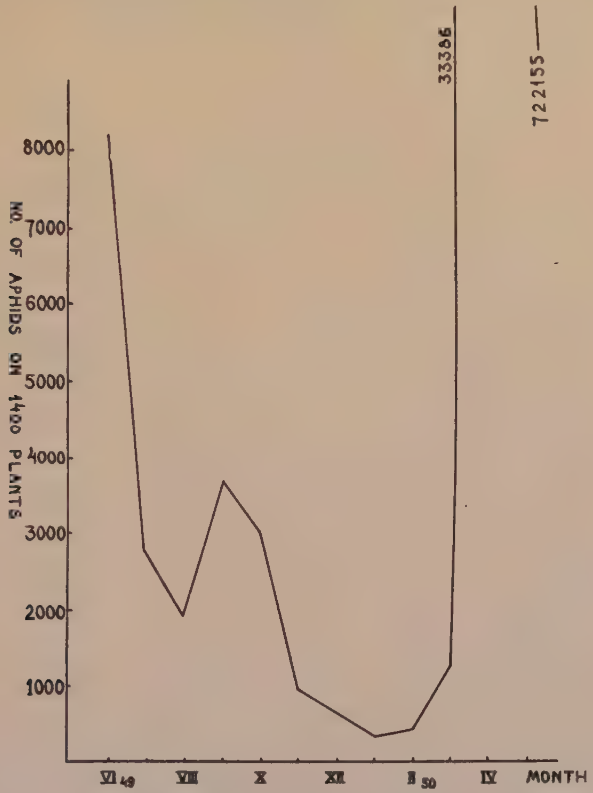


Fig. 2.—Fluctuations in population of *Hyalopterus pruni* on common reed at Wadi Rubin.

Effect of site.—Population changes on 1,000 plants, of which one half were growing in dry and the other half in wet soil, are shown in fig. 3. Plants growing in water and bog do not constitute congenial hosts for the Aphids and the population on such plants is generally less plentiful than in dry situations.

Seasonal variations.—The common reed flowers in Israel from July to November and produces abundant new growth in April and May. The aerial part of the plant survives the winter. The age of the leaves constitutes one of the factors which determine the susceptibility to infestation, the spring growth being the more vulnerable. The age of the leaves is not, however, the only controlling factor. Aphids can also be found on the older leaves, while the young ones frequently exhibit considerable immunity. Transfers of thousands of Aphids to laboratory plants yielded negative results, in spite of the availability of ample young growth. There are undoubtedly seasonal variations in the susceptibility of plants. The fact that certain plants are endowed with immunity creates difficulties in experimental infestation since failure does not necessarily indicate that a given species of plant is incapable of being a host. In experiments conducted with *H. pruni* and with other Aphids, attempts at inducing infestation were made on leaves from which the insects have been removed. It could thus be proved that, although the leaves were susceptible, the failure to induce infestation was entirely due to the fact that the plant was not a suitable host for the particular form of aphid (see below).

Ibbotson & Kennedy (1951) observed gregarious habits in *Aphis fabae* Scop. A similar tendency is exhibited by *H. pruni.*

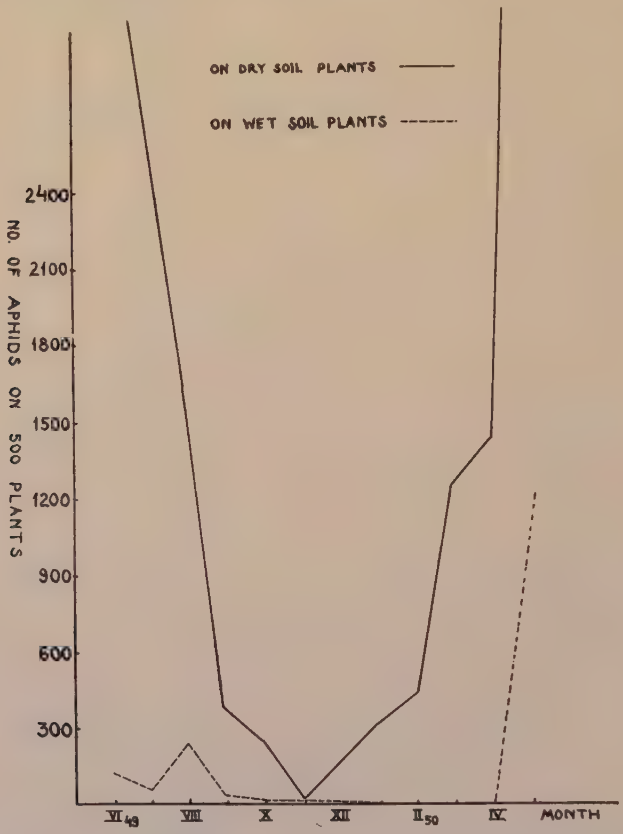


Fig. 3.—Fluctuations in population of *Hyalopterus pruni* on plants of common reed, growing in wet and dry soils.

On almond.

Twenty trees of the varieties Victoria, Greek, Nonpareil and Ne-Plus-Ultra (five trees of each variety) were selected for observation in an irrigated plantation at Miqve-Israel. A number of infested leaves were examined on each tree. An increase in the number of Aphids occurs in April and May and culminates in a maximum at the end of April or at the beginning of May (fig. 4).

Composition of the population.—The relative strength of apterous viviparous females is high in March and then it decreases with the overlapping of generations and the growing rate of reproduction (Table I). The alate forms which appear during the second half of April do not give rise to further broods on the almond, but migrate to reeds. The following tests were carried out to follow up their activities :—

1. On 30th April 1951, 50 alate viviparous females were put in bags (five per bag) which were subsequently tied over almond leaves cleared of insects. It was found a week later that all the Aphids had died without giving rise to

any larvae. This observation is in agreement with the findings of Smith (1936).

2. On 2nd May 1951, twenty bags containing 90 alate viviparous females were attached to disinfested leaves of common reed. At the end of a week the Aphids were still alive and had produced numerous larvae. After the lapse of an additional week the bags contained populous colonies of Aphids.

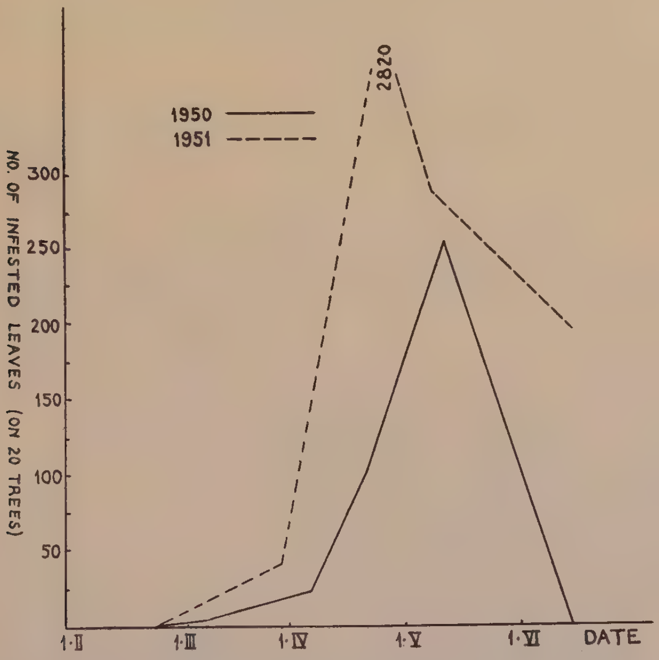


Fig. 4.—Fluctuations in population of *Hyalopterus pruni* on almond at Miqve-Israel in spring and early summer of the years 1950 and 1951.

TABLE I.

Percentage composition of the population of *Hyalopterus pruni* on almond at Miqve-Israel, during spring and early summer.

Date	Total number examined	Adult viviparous %		Larvae %
		Alatae	Apterae	
7.iii.1950	40	0	16·7	83·3
5.iv.	480	0	8·3	91·7
20.iv.	1160	5·2	10·3	84·5
10.v.	530	0·9	4·8	94·3
27.iii.1951	200	0	20·0	80·0
23.iv.	240	8·3	8·3	83·4
8.v.	200	2·0	5·5	92·5
14.vi.	250	0	8·0	92·0

Apterous forms can be found crawling upon the ground and on tree trunks. Formation of some new colonies takes place but the spread of the population is limited owing to non-participation of winged forms.

Phenology and varieties.—In irrigated orchards of the coastal plain, the varieties Victoria and Greek are more heavily attacked than Nonpareil and Ne-Plus-Ultra. The reasons for these varietal differences are discussed in the section dealing with *Brachycaudus amygdalinus.*

Climate.—In 1951 the peak in the population of *H. pruni* was attained in April, while in 1950 it was recorded in May. This is probably accounted for by the fact that the winter and spring temperatures in 1950 were lower in comparison with the following year (Table III).

Damage.—*H. pruni* accounts for serious injury to fruit trees in Israel. The Aphids congregate on the underside of the leaves and are responsible for curling and shedding of the foliage. This results in damage to the fruit and subsequent loss of crops.

Brachycaudus amygdalinus (Schout.).

Host-plants: Primary.—Almond; Secondary.—Horsetail knotweed (*Polygonum equisetiforme*).

Life-History.

The life-history of this Aphid was unknown in Israel and in other countries in which it occurs. The species was known to occur in spring on the almond and only spring forms had been described. Plaut (1949) encountered the Aphid on almond trees at Miqve-Israel from February to June. The activities of this species during the rest of the year remained unknown.

As a result of observations and experiments to be related below, it has been established that from the end of June until the end of October the almond is free of *B. amygdalinus*. *Gynoparae* and males arrive in November. The former give rise to oviparous females and these, in turn, lay eggs within crevices of the bark and in bud axils. The first eggs were laid in 1950 at the beginning of January. The Aphids congregate on the underside of the leaves and are responsible for curling and shedding of the foliage. *Migrantes* appear in April or May and depart from almond.

Aphids which had been found in 1947 on leaves and on shoots of the horsetail knotweed were thought at one time by Hille Ris Lambers to represent a new species. It has, however, been experimentally confirmed that the species is in fact *B. amygdalinus*, and thus the summer host of the pest has been found. *Alatae* from the almond were transferred in the spring of 1951 on to shoots of horsetail knotweed which had been cleared of Aphids. The *alatae* fed on the new host and produced larvae which later turned into *apterae* resembling those which occur naturally on knotweed. Horsetail knotweed is inhabited by the Aphids throughout the year. Counts indicate that in the coastal plain the population reaches its maximum in spring. The insects reproduce parthenogenically all the year round. Some males and *gynoparae* appear in autumn and migrate to almond. During the winter two parallel development cycles are pursued, a sexual cycle on almond and a parthenogenetic one on knotweed.

Fluctuations in Population.

Counts were carried out by the method described above (p. 626), using the same twenty trees at Miqve-Israel as in the case of *Hyalopterus pruni.* The number of curled leaves does not provide an indication of the extent of infestation, since the Aphids desert the dried-up leaves and move on to younger growth. It is necessary to uncurl the affected leaves and examine them for the presence of Aphids. In the spring of 1950 the peak in the population was recorded at the end of April while a reduction set in at the beginning of May. In 1951 the maximum was reached at the end of March, and the downward trend, which began in April, became more pronounced at the beginning of May (fig. 5). The Aphids disappeared completely from the almond trees by early June.

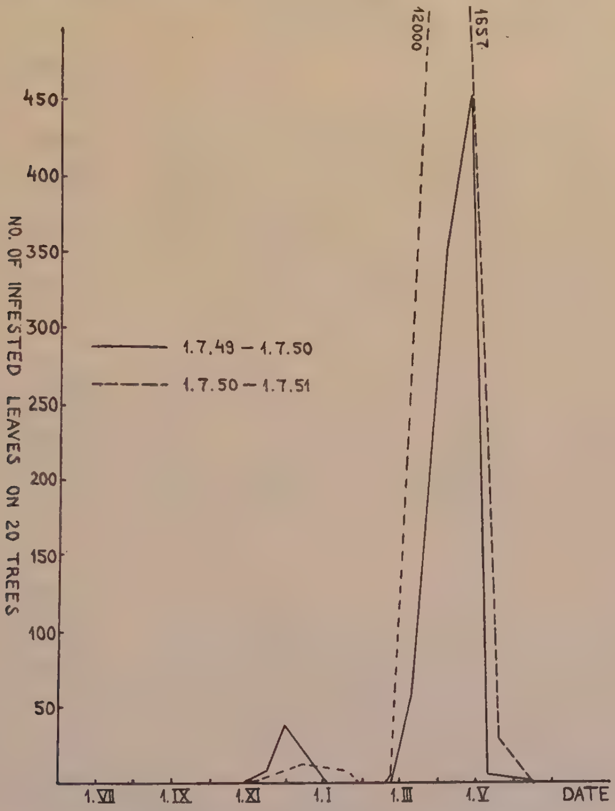


Fig. 5.—Fluctuations in population of *Brachycaudus amygdalinus* on almond at Miqve-Israel.

Composition of population.—As shown in Table II, alate viviparous females appeared in April and in May.

Attempts at artificially inducing infestation of young almond shoots in April 1950 gave negative results. The reliability of the experiment was, however, doubtful as there was no certainty concerning the appropriateness of the food provided. On 23rd April 1951 all apterous forms were removed from 15 infested leaves, leaving only the larvae of alatae. The larvae, numbering 48, were enclosed in silk bags. Examination at the end of one week revealed 30 live and ten dead *alatae* as well as eight live larvae. By the end of a fortnight from the beginning of the experiment, all the enclosed Aphids had died without leaving any progeny. These results prove conclusively that the winged forms produced in spring on almond do not migrate to other almond trees or reproduce on them, but transfer to some other host. A limited dispersion among almond trees is, however, effected by the wingless forms. Apterous viviparous females are responsible for the population growth on almond during spring. The percentage of these forms is high at the beginning of March. Subsequently, with the overlapping of generations and the increasing rate of reproduction, there is a proportionate increase in the numbers of juvenile forms.

Climate.—The average temperatures which prevailed in the years 1949–1951 during the months when almond is infested by Aphids are listed in Table III.

TABLE II.

Percentage composition of the population of *Brachycaudus amygdalinus* on almond at Miqve-Israel.

Date	Total number examined	Apterae %	Alatae %	Larvae %	Gyno-parae %	Males %	Ovip. females %	Ovip. females (larvae) %
15.xi.1949 ..	7	0	0	0	100·0	0	0	0
29.xi. ..	40	0	0	0	50·0	30·0	0	20·0
7.iii.1950 ..	47	19·1	0	80·9	0	0	0	0
23.iii. ..	220	9·1	0	90·9	0	0	0	0
5.iv. ..	500	8·0	0	92·0	0	0	0	0
20.iv. ..	480	10·0	9·0	81·0	0	0	0	0
10.v. ..	50	9·0	0·9	90·1	0	0	0	0
9.xi. ..	5	0	0	0	100·0	0	0	0
14.xii. ..	50	0	0	0	52·0	39·5	0	8·5
29.xii. ..	20	0	0	0	50·0	28·0	10·0	12·0
18.i. 1951 ..	20	0	0	0	20·0	30·0	30·0	20·0
25.ii. ..	13	0	0	100·0	0	0	0	0
27.iii. ..	332	12·6	0	87·4	0	0	0	0
23.iv. ..	500	14·8	1·2	84·0	0	0	0	0
17.v. ..	200	8·0	0	92·0	0	0	0	0

TABLE III.

Average monthly temperatures in °C. recorded at Rehovot from November to May (1949–50 and 1950–51).

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
1949–50	19·2	14·3	10·3	11·6	15·0	16·4	19·8
1950–51	19·1	17·6	14·0	14·3	17·2	19·1	22·6

The months of December 1949 and January 1950 were cold and rainy (259·8 mm. rain in December at Rehovot). The sexual forms disappeared at the beginning of January. In the winter of 1950–51 these two months were warm and dry (19·3 mm. rain in December). The sexual forms disappeared only at the end of January. The hatching of the eggs in 1951 took place at the beginning of February, and under the cooler conditions of 1950 a fortnight later. Similarly, the maximum population was recorded in April of 1950, whereas in 1951 the maximum was attained in March.

Phenology and varieties of almond.—The production of a strong spring generation of Aphids depends on the following properties of the host tree: (a) proneness to autumn infestation, which implies the presence of leaves and being in a suitable condition, (b) adjustment between the time of egg-hatching and the resumption of tree growth, (c) susceptibility of the variety to spring infestation. The varieties Nonpareil and Ne-Plus-Ultra, as opposed to Victoria and Greek, do not meet the first two requirements. At the end of February 1950 and again at that time in the following year, the buds of Nonpareil were still tightly closed, so that, even where eggs had been laid, the hatched larvae died of starvation. The dormancy of Ne-Plus-Ultra is broken by the end of February, but the amount of new growth is still very small. The varieties Victoria and Greek, on the other hand, are in full growth during the second half of February and are thus phenologically well adapted to the requirements of the Aphids.

Damage.—The injury to almond trees is very considerable. The Aphids congregate on the underside of the leaves and are responsible for curling and shedding of the foliage.

Aphanostigma piri (Chol.).

Examination of specimens of *Cinacium iaksuiense* Kishida which had been kindly supplied by Dr. Yasumatsu, revealed morphological differences between the Japanese species and *Aphanostigma piri*. According to Schweig (1950) Aphids of the latter species abound in the autumn and are responsible for cracking of the bark of pear trees which may result in the death of affected branches.

Life-History.

The Aphids were found by the author (1950) in the winter of 1950 in the buds of pear trees and in summer of the same year in cracks of the bark. They remain in these places throughout the year. It follows that they are capable of uninterrupted parthenogenetic reproduction. In fact, sexual forms have not yet been discovered in this country, although the existence of a sexual cycle during autumn and winter was established by Cholodkovsky (1903) in the Crimea and by Roberti (1948) in Italy.

Fluctuations of Population.

Tanabe & Mishima (1930) employed belts in their population studies. This method is only of value in those areas where the life-cycle of the Aphids and their whereabouts are known at all seasons. The lack of any previous phenological information, in relation to this species under conditions in Israel, precluded the use of any artificial observation methods. A direct study of the Aphids on different parts of the tree was therefore undertaken.

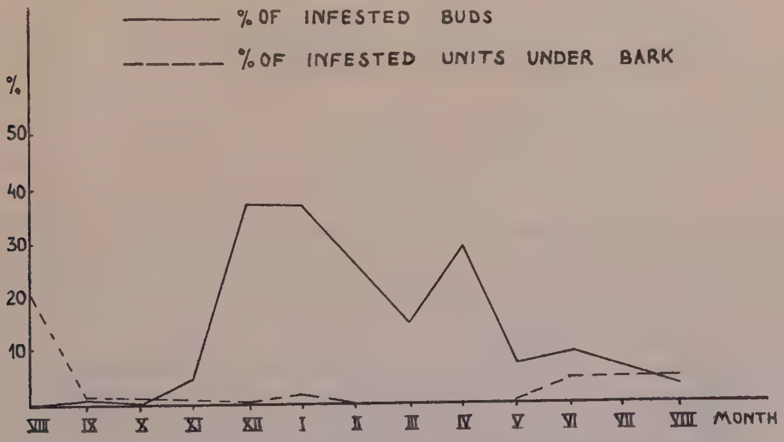


Fig. 6.—Fluctuations in population of *Aphanostigma piri* on the variety Superfine at Miqve-Israel, during the period August 1950–August 1951 (in buds and under bark).

Bark crevices.—At Ein-Harod (eastern Esdraelon valley), concentrations of Aphids were observed throughout the year in crevices of the bark of Spadona and Coscia varieties of pears. A small colony was also discovered after a prolonged search on the variety Gentil. At Kiryath Anavim (Judaean Hills) the Aphids were found on the variety Epargne all the year round. At Miqve-Israel (coastal plain), counts were made on the varieties Superfine and Artas; 100 bark sections, each covering 4 sq. cm., were opened up and examined each month. The population was found to reach its peak in autumn (figs. 6, 7).

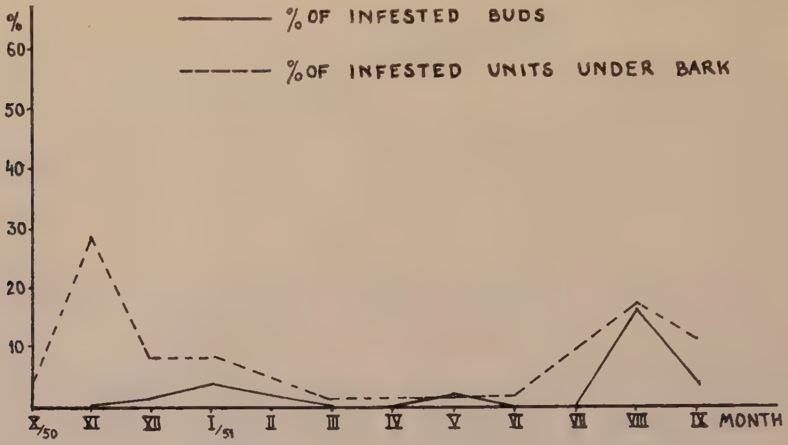


Fig. 7.—Fluctuations in population of *Aphanostigma piri* on the variety Artas at Miqve-Israel, during the period October 1950–September 1951 (in buds and under bark).

Bark surface.—Counts were made at Ein-Harod on the following parts of a Spadona pear tree; stem, 3 boughs, 70 branches, 100 spurs. The colonies were classified according to the number of Aphids, 1 (1–5), 2 (6–10), 3 (11–20), 4 (over 20). The population was found to attain its peak in December (Table IV). The northern and eastern sides of the tree are more susceptible, due to the direction of the prevailing wind. The variety Spadona is more liable to attack than Coscia and Gentil.

In the coastal plain, bark infestations were recorded on the following varieties, Superfine, Beurrè-Giffard, Artas, Kieffer, Flemish-Beauty, Bergamote, Clapps and Epargne.

TABLE IV.

Fluctuations in population of *Aphanostigma piri* on Spadona variety of pear at Ein-Harod, from December 1950 to December 1951 (on bark).

Month	Number of colonies				Total
	1	2	3	4	
Dec. 1950	590	105	69	14	778
Jan. 1951	207	35	10	0	252
Feb.	146	34	6	0	186
Mar.	117	43	3	0	163
Apr.	55	99	24	0	178
May–Nov.	0	0	0	0	0
Dec.	5	0	0	0	5

It was noted that vacant scales of *Parlatoria oleae* (Colv.) provide a convenient home for the Aphids.

Buds.—It is a well-known fact in Israel that a considerable proportion of the buds of the Superfine pear fails to open in spring. Some of these buds were found to contain Aphids throughout the year. The Aphids abound particularly in winter and early spring (figs. 6, 8). Opening buds are easily penetrated and destroyed. Tightly packed, dormant buds, on the other hand, offer considerable resistance to any but the most superficial attack. The development and breaking of Superfine buds seem to follow an abnormal course in this country. Fruit buds are formed in summer, swell as early as September, and in October they open partly and sometimes even blossom and break into leaf. Such precocious buds are easily penetrated and destroyed by the young *Aphanostigma* larvae. It should be noted, however, that many buds fail to open for reasons other than aphid attack.

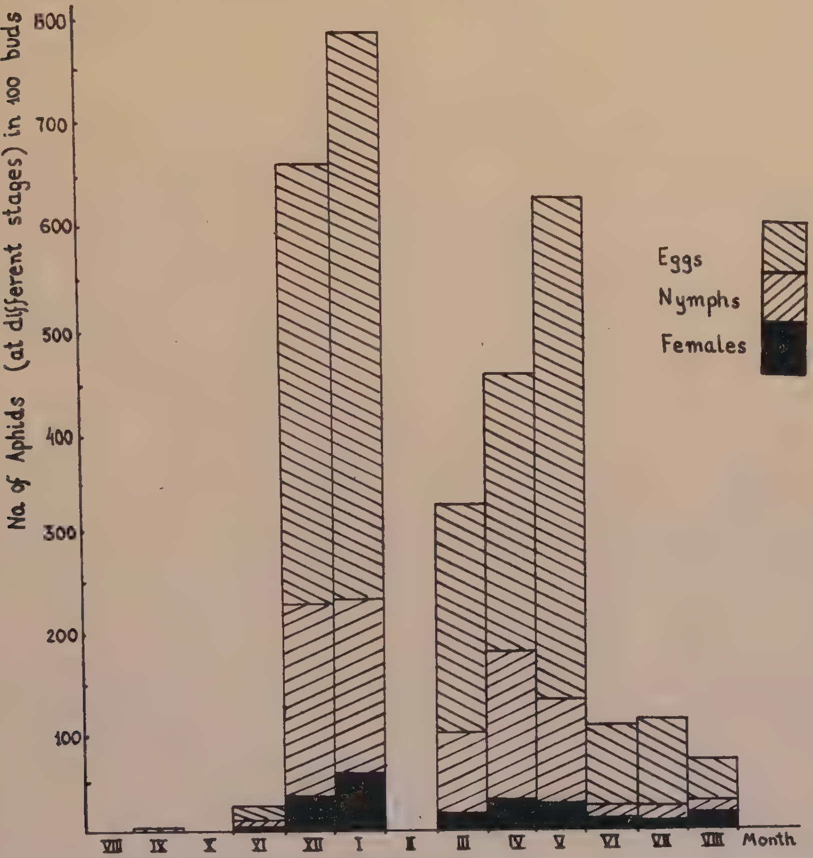


Fig. 8.—Fluctuations in population of *Aphanostigma piri* in buds of the variety Superfine at Miqve-Israel, during the period August 1950–August 1951.

The Aphids are abundant in the buds of the variety Artas at the end of summer and in autumn (fig. 7). This variety is, however, considerably less susceptible than Superfine. The susceptibility of the variety Ein-Harody is somewhere between that of Artas and Superfine, while Bartlett Sport, Triomphe de Vienne, Forrel, and Pineapple are subject to only slight attacks.

The location of the infestation on the tree depends on its age, the condition of the bark, the position of the buds, etc. Fruits do not become infested in Israel. It is believed that the covering of fruits with bags is conducive to infestation in that it provides a convenient shelter for the Aphids. This practice is uncommon in this country.

Damage.—The injury to pear trees is very considerable. The Aphids are responsible for cracking of the bark of pear trees, which may result in the death of affected branches, and for the destruction of many buds.

Miscellaneous Species.

Myzus persicae (Sulz.) affects in Israel, among fruit trees, *Citrus*, quince, pear, apple, almond, apricot, myrobalan and Japanese plum. On wild plants, vegetables and ornamentals the Aphids reproduce parthenogenetically throughout the year (Bodenheimer, 1930; Klein, 1943; Swirski, 1947). A sexual generation occurs on apple. Alate viviparous females migrate in spring to apple, where they reinforce the existing population. In May, the apple trees are abandoned and remain free of Aphids until late autumn. Pear, plum, apricot and almond are invaded in the spring by the viviparous forms. Damage to fruit trees in Israel is slight.

Colonies of *Ovatus mespiliella* (Theob.) were found in January 1951 on local varieties of apple.

Occasionally, in spring, leaves of deciduous fruit trees (apple, pear, plum) are infested to some extent by *Aphis craccivora* Koch and *A. gossypii* Glov. These species can breed parthenogenetically throughout the year on vegetables and ornamental plants (Bodenheimer, 1930; Klein, 1943; Swirski, 1947). No sexual forms have yet been found in this country. The Aphids desert the fruit trees when the foliage is fully grown. *Aphis gossypii* is found in small numbers on pomegranate. Fairly heavy infestations occur in some years on guava trees, the attacks being largely confined to younger leaves.

Led

Aphis pomi Deg. was found in this country on apple, pear and quince. The life-history, as described by Plaut (1949) agrees with that obtaini~~ng~~ in other countries. Parthenogenetic breeding in spring, summer and autumn is followed by sexual reproduction in late autumn and winter. Males and oviparous females appear in November and the percentage of males is low. A rather similar picture was presented by Baker & Turner (1916) and by Nevskiĭ (1929). The hatching of eggs in 1951 at Rehovot was recorded in March. The maximum infestation of apple trees was recorded in the coastal plain in summer and was followed by a reduction in autumn. The viviparous females and their larvae show a preference for young leaves and thus the amount of suckers around the tree trunks has an effect on the size of population. *Stephanitis piri* (F.) (TINGIDAE), which appears in large numbers at the end of summer, has a depressing effect on aphid population, since leaves which have already been sucked by this lace bug are not frequented by the Aphids. In the Judaean Hills, apple trees are mostly grown without irrigation and produce little new growth in the summer. Consequently there is little aphid infestation. Losses are very considerable, however, in some places and in certain seasons.

Aphis punicae Pass. infests in this country pomegranate and *Duranta plumieri*. A parthenogenetic cycle is pursued on pomegranate during spring, summer and early autumn. In December and January males and oviparous females make their appearance and they concentrate on the few leaves which still remain on the tree. Eggs are laid in bud axils. In 1950 and 1951 the eggs hatched in the coastal plain during March. On *Duranta*, reproduction is parthenogenetic. Here again is a case of two parallel development cycles during the winter: amphigonic on *Punica* and parthenogenetic on *Duranta.* Willcocks (1922) found the sexual forms of *A. punicella* Theob. in Egypt. If this species is synonymous with *A. punicae*, that would point to the existence of an amphigonic cycle of the latter species in Egypt. The maximum infestation of pomegranate occurs in the spring, and a summer depression is again followed by a slight rise in the autumn. Summer irrigation enhances the amount and vigour of vegetative growth and thus increases the susceptibility to aphid attack. Thus irrigated pomegranates at Miqve-Israel (coastal plain) and at Ein-Harod (Esdraelon valley) suffered heavier infestations than unirrigated plantations of Kiryath Anavim (Judaean Hills). Infestations of *A. punicae* result in the formation of a sooty covering on the twigs, leaves and fruits. This interferes with the normal development of the trees and renders the fruit unfit for market.

A. ruborum Börner breeds parthenogenetically on the local bramble (*Rubus ulmifolius*). No sexual forms have been discovered. The Aphids show preference for the young growth and they frequently penetrate into the upper layers of the soil, in pursuit of the bramble runners. The population attains its maximum in spring, while the minimum is reached in summer. The availability of new growth on the host-plant appears to be the controlling factor.

The principal hosts of *Toxoptera aurantii* (Boy.) are citrus trees. Rivnay (1938) maintains that the reproduction of this species is parthenogenetic, and only a few males were found by him in this country. The undersides of leaves of apple and pear are sometimes slightly affected in spring.

In certain seasons and localities considerable damage to apple leaves is caused by *Sappaphis plantaginea* (Pass.). It is likely that other species are also involved, but according to Dr. Hille Ris Lambers they would appear to be closely allied to *S. plantaginea.* An amphigonic cycle is maintained on apple in winter (November–February) and is followed by a number of parthenogenetic generations (March–June). It is yet unknown what happens to the Aphids in summer. A colony was discovered by the writer (1947) on the snapdragon.

The life-history of *Chromaphis juglandicola* (Kalt.) in Israel resembles that known in Europe, California and central Asia. Alate viviparous females and their larvae spend the spring, summer and early autumn on the underside of walnut leaves. Males and oviparous females appear during the last two months of the year. The eggs laid by the females hatch the following spring. The population is greatest in late spring and early summer and there is another lower peak in early autumn. *Retithrips syriacus* (Mayet) competes with the Aphids in late summer, since leaves visited by the thrips are rendered unsuitable as food for the Aphids. No serious losses have been recorded so far in this country.

Eriosoma lanigerum (Hsm.) was studied by Bodenheimer (1947) and *Lachnus persicae* Chol. by Plaut (1949).

Predators and Parasites.

Ladybirds are active in the colonies of *Hyalopterus pruni* and *Brachycaudus amygdalinus* throughout the spring. The following species have been found: *Coccinella 7-punctata* L., *C. conglobata* L., *Scymnus syriacus* Mars., *Chilocorus bipustulatus* (L.), *Exochomus 4-pustulatus* (L.), *E. flavipes* (Thnb.). Among the colonies of *Hyalopterus* on reed they were present in rather insignificant numbers. Ladybirds of the species *Coccinella 7-punctata*, *C. conglobata* and *Thea bisoctonotata* (Muls.) were found at the end of spring in considerable numbers among the colonies of *Aphis punicae*. *Coccinella 7-punctata* has been found to prey upon *Aphanostigma piri* in autumn, but it does not appear to exercise a decisive control.

Larvae of *Phaenobremia* sp. (CECIDOMYIIDAE) appear in March among the colonies of *Hyalopterus pruni* and *Brachycaudus amygdalinus* on almond. The incidence of the predator is still low in this month, and rises to a maximum in April or May. When present in large numbers, these larvae are capable of completely eliminating large concentrations of Aphids. Since, however, they only attain numerical strength in April and early May, their depredations are largely confined to those Aphids which remain on the almond trees after the departure of the winged migrants and thus cannot be regarded as a primary cause of the drop in population. These larvae appear to be the major factor amongst predators controlling the size of the population of *Aphis punicae*.

Small concentrations of larvae of Syrphid flies could be detected in the colonies of *Hyalopterus pruni* on reed throughout the year. Among the colonies of *Brachycaudus amygdalinus* and the former species on almond they were found in large numbers from March onwards. The most prevalent species was *Lasiopticus seleniticus* (Mg.). Since these predators appear earlier than the Cecidomyiids, they still catch up with the rising trend in the aphid population. Small numbers of larvae were observed to prey upon *Aphis punicae* in spring and summer.

Ochtiphilid and Trombidiid larvae were present among the colonies of Aphids in rather insignificant numbers. *Leucopis puncticornis* Mg. is mentioned by Plaut (1949).

The highest percentage of parasitised *Hyalopterus pruni* was found in the years 1947–48 (Plaut, 1949) and 1949–51 during May. The percentage of parasitised *Brachycaudus amygdalinus* at Miqve-Israel was low in the years 1950–51. Plaut (1949) found that in the years 1947–48 the number of parasitic wasps was low in February and highest in April.

Predators and parasites exert some control, but do not appear, on the whole, to be decisive in bringing about critical reductions in the size of the population.

Summary.

The species of Aphids dealt with in this paper can be divided into several groups, according to their life-history.

Aphis pomi Deg., *Aphis punicae* Pass. and *Chromaphis juglandicola* (Kalt.) have a life-history similar to that obtaining in Europe. It consists of a parthenogenetic cycle in spring, summer and early autumn, and a sexual cycle in late autumn and winter. The parthenogenetic cycle of *A. punicae*, pursued in the winter on *Duranta*, runs simultaneously with a sexual cycle on pomegranate.

Aphis ruborum Börner is capable of parthenogenetic reproduction on bramble throughout the year.

Hyalopterus pruni (Geoff.), *Brachycaudus amygdalinus* (Schout.) and *Myzus persicae* (Sulz.) reproduce parthenogenetically on herbaceous plants all the year round. The invasion of fruit trees occurs in autumn, whereupon an amphigonic cycle is pursued on the trees. Several parthenogenetic generations are produced in the spring, until the emergence of alate forms which migrate to the appropriate herbaceous host and reinforce the population already present there. *M. persicae* invades fruit trees in spring also.

Aphis gossypii Glov., *Aphis craccivora* Koch and *Toxoptera aurantii* (Boy.) produce a few parthenogenetic generations on deciduous fruit trees during spring.

Sappaphis plantaginea (Pass.) (*s. l.*) starts the season with a sexual generation and then breeds parthenogenetically until early summer. All this development takes place on apple trees.

Aphanostigma piri (Chol.) is capable of all-the-year-round parthenogenetic reproduction. No sexual forms have yet been found in Israel. The Aphids hide mostly in bark crevices and in buds of pear trees, but at times of intensive reproduction (mainly in autumn) they abound on the surface of the bark.

The size of the population of the aphid species dealt with has been found to be determined by weather, the condition of the host and by cultural treatments, such as irrigation. Predators and parasites exert some control, but do not appear,

on the whole, to be decisive in bringing about critical reductions in the size of the population.

Parasites and predators are referred to and their influence on the aphid populations discussed.

Acknowledgements.

The author wishes to express his thanks for assistance offered by Prof. F. S. Bodenheimer. The work was carried out in the Department of Dr. Z. Avidov (Klein) at the Agricultural Research Station, Rehovot. Dr. D. Hille Ris Lambers identified many of the species of Aphids from Israel. Dr. K. Yasumatsu supplied specimens of *Cinacium iaksuiense* and was very helpful in collecting and translating relevant Japanese literature. Dr. G. Wertheim and Dr. I. Harpaz have rendered valuable assistance in securing literature and materials.

Mr. J. P. Doncaster has been kind in many ways and has been good enough to look over the manuscript of this paper and provide much valuable advice. The author's thanks are due to all these persons.

References.

Baker, A. C. & Turner, W. F. (1916). Morphology and biology of the Green Apple Aphis.—J. agric. Res., **5**, pp. 955–994.

Bodenheimer, F. S. (1930). Die Schädlingsfauna Palästinas.—Monogr. angew. Ent., **10**, 438 pp.

Bodenheimer, F. S. (1935). Animal Life in Palestine.—507 pp. Jerusalem, Mayer.

Bodenheimer, F. S. (1937). Prodromus faunae palaestinae.—Mém. Inst. Egypte, **33**, 286 pp.

Bodenheimer, F. S. (1947). Studies on the physical ecology of Woolly Apple Aphis (*Eriosoma lanigerum*) and its parasite *Aphelinus mali* in Palestine. —Bull. agric. Res. Sta. Rehovot, no. 43, 20 pp.

Cholodkovsky [Cholodkovskiĭ], N. (1903). Aphidologische Mitteilungen.— Zool. Anz., **27**, pp. 118–119.

Das, B. (1918). The Aphididae of Lahore.—Mem. Indian Mus., **6**, pp. 135–274.

Hall, W. J. (1926). Notes on the Aphididae of Egypt.—Bull. Minist. Agric. Egypt, no. 68, 62 pp.

Hille Ris Lambers, D. (1948). On Palestine Aphids.—Trans. R. ent. Soc. Lond., **99**, pp. 269–289.

Ibbotson, A. & Kennedy, J. S. (1951). Aggregation in *Aphis fabae* Scop. I. Aggregation on plants.—Ann. appl. Biol., **38**, pp. 65–78.

Klein, H. Z. (1941). Pests of vegetables. [In Hebrew.]—Tel-Aviv.

Klein, H. Z. (1943). Survey of orchard pests in Palestine in 1942. [In Hebrew.] —Hassadeh, **23**, pp. 147–149.

Nevskiĭ, V. P. (1929). The Aphids of Central Asia. [In Russian.]—[Publ.] Uzbek. exp. Pl. Prot. Sta., no. 16, 424 pp.

Plaut, N. (1949). Ecological and biological studies on Aphids in Israel. [In Hebrew.]—Jerusalem.

Rivnay, E. (1938). Factors affecting the fluctuations in the population of *Toxoptera aurantii* Boy. in Palestine.—Ann. appl. Biol., **25**, pp. 143–154.

Roberti, D. (1948). Contributi alla conoscenza degli afidi d'Italia, V. *Aphanostigma piri* (Cholodk.).—Boll. Lab. Ent. agr. Portici, **8**, pp. 91–99.

Schweig, K. (1950). Pests of vine and fruit-trees. [In Hebrew.]—Tel-Aviv.

Smith, L. M. (1936). Biology of the Mealy Plum Aphid, *Hyalopterus pruni* (Geoffroy).—Hilgardia, **10,** pp. 167–209.

Swirski, E. (1947). Plant Lice of ornamental plants in Palestine. [In Hebrew.] —Jerusalem.

Swirski, E. (1950). Observations on *Aphanostigma piri* Chol. (Aphidoidea: Phylloxeridae) in pear buds in Israel. [In Hebrew.]—Hassadeh, **30,** p. 655.

Tanabe, C. & Mishima, R. (1930). Results of the studies on *Cinacium iaksuiense* Kishida (Phylloxeridae). [In Japanese.]—183 pp. Nara, Nara agric. Exp. Sta.

Willcocks, F. C. (1922). A survey of the more important economic insects and mites of Egypt.—Bull. sultanic agric. Soc., no. 1, 483 pp.

RESPONSES OF PESTS TO FUMIGATION.

V.—THE TOXICITY OF THE FREE AND SORBED VAPOURS OF BHC AND DDT TO SOME INSECTS INFESTING STORED PRODUCTS.*

By M. Maqsud Nasir.

Imperial College Field Station, Sunninghill, Berks.

When contact insecticides, such as the chlorinated hydrocarbons, BHC and DDT, used in this investigation, are applied to surfaces near infested commodities, they may affect insects within the stored product in one of two ways. The first possibility is that the vapours from the insecticidal coating may be sorbed by the stored products, due to a slow transfer of the insecticide from the original site of application on the sack. This process has been described for DDT and BHC by a number of authors (*e.g.*, Butterfield & others, 1949). Page & Blackith (1953) have recently reviewed some chemical investigations on this subject. The transfer of an insecticidal deposit to a porous or granular substrate has a parallel in the work of Hadaway & Barlow (1952) who found that DDT and γ BHC, applied superficially to mud blocks, were eventually almost quantitatively removed to the substrate by progressive sorption.

Once sorbed into a bagged commodity in this way, an insecticide may be important either because of its toxicity to insects feeding or living in the commodity, or because of its taint or the toxicity to consumers of the stored product.

A second possible action of an insecticide so applied is the direct fumigating action of the vapour. Many authors have reported that γ BHC acts in this way, and Nasir (1947) has reported that a commercial specimen of DDT could exert such a fumigant action, although there are no reports known to the writer of p,p′DDT being active in this way. Pure p,p′DDT has a considerably lower vapour pressure than γ BHC. According to Balson (1947) the values at 30°C. are $7{\cdot}2 \times 10^{-7}$ mm. and $4{\cdot}5 \times 10^{-5}$ mm., respectively. Losses in weight of DDT films after prolonged storage have been reported but in at least some instances this loss seems to have been associated with the volatilisation of an impurity, rather than of the DDT itself. (Wichmann & others, 1946.)

The objects of the work presented in this paper were twofold. Firstly, an extension of the work of Butterfield & others (1949) on the transfer of DDT vapour from sacking to stored products, with particular reference to biological tests. These authors described the transfer as on such a scale that it is unsafe to store ground or broken foods in sacks impregnated with 1 per cent. DDT for more than four months. The importance of this is evident.

The second object is to describe experiments on the toxicity of DDT and BHC in the vapour phase, with particular reference to the occurrence of a volatile impurity in commercial specimens of DDT.

Transfer of DDT and BHC to Grain, Flour and Groundnuts.

Samples of whole English wheat (25 gm.), flour (6 gm.) and decorticated groundnuts (15 gm.) were placed separately in circular trays of wire gauze, 3 inches in diameter and 0·4 in. deep. Trays intended to contain flour were lined with filter paper. The gauze tray was supported on three legs and stored in a petri dish so that it rested 0·3 in. from the bottom of the dish. A small tin receptacle, 2·4 inches in diameter, and 0·1 in. high was used to contain the insecticides which were to provide vapour. These tin receptacles contained 0·3 gm. γ BHC, 0·1 gm. pure p,p′DDT (m.p. 107·5°C.) or 0·8 gm. of a sample of commercial DDT with setting point 90·5°C., each spread evenly over their appropriate receptacles, which were then placed under the gauze tray in the petri dish, which was kept sealed for six months in a constant temperature of 27°C. Two sets of dishes were prepared containing wheat, in order to compare grains of 10 per cent. moisture content with those containing 14 per cent. The moisture content of grain over this range is known to be of great importance in determining the sorption of vapours.

---

* Part of a thesis approved by the University of London for the Ph.D. degree.

The stored materials were then removed from the gauze trays and their toxicity to insects estimated by the following methods:

Treated wheat, assayed with Calandra granaria *(L.).*

Grains of wheat of both moisture contents were fed to 1- to 2-week old adult *C. granaria* in specimen tubes under two conditions. In one experiment 150 grains were placed in a 3 × 1 in. specimen tube, the cork of which was replaced by muslin. In another, 50 grains were placed in a smaller 2 × ½ in. tube, which was kept corked throughout the observation period. There were 15 insects in each tube, and four replicate tubes were prepared in each category. All tubes were maintained at 27°C. and about 70 per cent. R.H. Table I gives the mean time taken to kill 50 per cent. of the insects feeding on the grain. Although this is only a very rough measure of the toxicity of the grains, Table I discloses the marked differences between the three insecticide treatments. It is evident that even p,p′DDT is sufficiently volatile to affect grain stored in the way described, and that the commercial DDT is of rather greater effectiveness. BHC, as expected, is the outstanding insecticide in this test. Indeed, even when, in a separate experiment, small cages containing ten adult weevils were suspended inside the closed specimen tubes containing the BHC-treated grains, so that the insects could not feed on, or touch, the grain, they were all killed within a few hours by the vapour desorbed from the wheat.

TABLE I.

Toxicity to *Calandra granaria* of wheat stored in vapours of contact insecticides. (Mean time taken to kill 50% of the test insects is shown.)

Insecticide	Moisture content %	Open tubes	Closed tubes
p, p′ DDT ..	10	20 days	10 days
	14	20 days	10 days
Commercial DDT	10	< 7 days	< 7 days
	14	< 7 days	< 3 days
γ BHC ..	10	< 5 hours	< 5 hours
	14	< 5 hours	< 5 hours
Untreated grains	10	>30 days	*
	14	>30 days	*

* Grains went mouldy after 27 days, at which time the test insects appeared normal.

There was no noticeable difference either between wheat of the two moisture contents chosen, or between open and closed testing conditions. There was, however, one material difference between the open and closed tubes containing grain treated with commercial DDT or with the pure compound, of a kind which does not show in Table I. In the open tubes only, the weevils inserted as test insects laid eggs which developed normally, giving rise to a fresh generation after some 58 days, this new generation being apparently unaffected by the insecticides. Control tubes containing other insects suggest that development is inhibited in this closed environment so that these results should be treated with reserve.

Treated wheat, assayed with Sitotroga cerealella *(Ol.)*.

The experiments using *S. cerealella* as test insect differed in only two respects from those using *C. granaria*. In the open tubes, the number of fumigated grains was reduced to 75, and 75 newly-hatched larvae were placed in each tube. In the closed tubes 25 larvae were introduced. Table II gives the proportion of larvae which succeeded in developing to adult moths after 50 days from the time of their introduction. As in experiments with weevils, the biological measure of toxicity is a rough one, but, as the figures in Table II represent four replicated experiments, they serve to indicate the general order of toxicity of the fumigated grains. It is not easy to see what additional useful information would be obtained from the use of more refined methods in this instance.

TABLE II.

Toxicity to *Sitotroga cerealella* of wheat stored in vapours of contact insecticides. (The proportion of introduced larvae developing to adults in 50 days is shown.)

Insecticide	Moisture content %	Open tubes	Closed tubes
p, p′ DDT ..	10	47, 40, 44, 31	20, 16, 12, 8
	14	29, 20, 27, 16	24, 16, 4, 0
Commercial DDT	10	0, 0, 0, 15	4, 0, 4, 4
	14	60, 48, 27, 39	4, 4, 0, 24
γ BHC ..	10	0, 0, 0, 0	0, 0, 0, 0
	14	0, 0, 0, 0	0, 0, 0, 0
Untreated grains	10	77, 52	32, 40
	14	60, 67	28, 40

With the grain moths, there is a marked reduction in the proportion of successfully developing larvae in the closed tubes, even in the controls on untreated grain. In other respects the results confirm those obtained with weevils, namely, that pure DDT produces an appreciable toxic effect which is enhanced when the commercial product is used, and that BHC causes the death of all the introduced insects.

The causes of the discrepancies between the results of tests of *Sitotroga* larvae with wheat stored in the vapours of commercial DDT are not clear, in particular there seems no obvious explanation for the low mortalities obtained with wheat of 10 per cent. moisture content in open tubes.

Treated flour, assayed with Tribolium confusum *Duv.*

In these experiments 1·5 gm. of the treated flour replaced the wheat in the open tubes and half that quantity was used in the closed tubes. Flour of 14 per cent. moisture content was slightly mouldy after the six months storage over the insecticides. The four replicates, prepared as in the preceding experiments, were this time divided into two pairs, one receiving ten *Tribolium* eggs, the other receiving ten newly-hatched larvae. In the closed tubes, development in either case was poor in the controls, and completely inhibited in all tubes containing treated flour, although eggs hatched in all tubes. With those tubes left open during the experiments, development to the adult stage was good in the controls, but completely inhibited with BHC-treated flour, even to the suppression of "gallery" formation by the first-instar larvae. With pure and commercial DDT, the larvae lived long enough to show gallery formation, although most individuals died during the first instar and only a few dead insects were found to be in their second instar. In only one tube, containing flour treated with vapour from pure DDT, was one adult insect observed.

Treated groundnuts, assayed with Tribolium confusum *and* Oryzaephilus surinamensis (*L.*).

Open tubes only were used in this work, in which three groundnut kernels were used as a substrate for 15 adult *T. confusum* or, in another series of tests, for 15 adults *O. surinamensis* (3–4 weeks old). The usual four replicates of each treatment were done (Table III).

TABLE III.

Toxicity of groundnut kernels, stored in vapours of contact insecticides, to *Tribolium confusum* and *Oryzaephilus surinamensis*. (Percentage mortality after 22 days exposure is shown.)

Insecticide	*T. confusum*	*O. surinamensis*
p, p′ DDT ..	60, 80, 33, 20	13, 20, 7, 40
Commercial DDT ..	60, 27, 53, 40	13, 53, 53, 13
γ BHC ..	100, 100, 100, 100	33, 20, 13, 33
Untreated controls ..	13, 40, 27, 40	20, 27, 0, 0

With *Tribolium* as test insect, complete control is attained with BHC, and both types of DDT produce higher mortalities than occur on unfumigated groundnuts. Moreover, although some young larvae hatched from eggs laid in the control tubes, none was observed in any treated kernels. Adults of *O. surinamensis* showed a higher mortality on all the treated groundnuts than in the controls, but BHC did not, in this instance, kill the adult beetles. Larvae were found, however, in the control and DDT treatments, but not in tubes with BHC-treated groundnuts, after 30 days.

Direct Fumigant Action of Contact Insecticide Vapours.

Davidson & Burnett (1952) have emphasised that unless rigorous exclusion of particulate matter is ensured, a number of contact insecticides may give rise to apparent fumigating action in an airspace. After passage over an insecticide, air may be filtered through a plug packed with some such filter as asbestos. The introduction of an efficient filter raises the difficulty that, in view of the small mass of vapour in the gas system in equilibrium with such sparingly volatile insecticides, a substantial fraction may be sorbed on the filter or connecting glass apparatus. This possibility was overcome by running two sets of tests.

One set was carried out inside a closed tube lined with filter paper impregnated with the insecticide under examination. Because of the susceptibility of most test insects to dehydration the air was conditioned over a saturated sodium chloride solution to give a relative humidity of about 70 per cent. A copper gauze cage, 7 in. long and of 0·8 in. diameter, was fitted with distance pieces to enable it to be lowered into the tube lined with insecticide without receiving contamination from the side, and clearing the sodium chloride solution in the bottom of the tube. Four small insect cages were suspended from wires inside the outer cage, which was used to keep the small cages from swinging against the impregnated lining of the tube, which in turn was closed by a cork covered with aluminium foil prior to the insertion of the test insects through narrow holes, a process which did not disturb the contained air. The tube was conditioned at 27°C. for 72 hours to ensure saturation.

The results of this set of tests are shown in Table IV. As many other workers have shown, BHC vapour rapidly killed both grain weevils and moths. Of considerable interest is the fact that commercial DDT proved lethal to these insects almost as quickly as BHC, although p,p′DDT had little action inside eight hours. A similar experiment was made using, instead of adult insects, the eggs of *Sitotroga cerealella*, laid on tissue paper, and of *Tribolium confusum* laid on flour but collected and pasted on tissue paper. Both sets of eggs were maintained in the fumigating apparatus until control batches had completed hatching. It appears, from Table V, that although *T. confusum* eggs are indifferent to the insecticide vapours, BHC exerts a considerable ovicidal action on the eggs of *S. cerealella.* A second set of experiments was carried out in which the vapours of the insecticides were allowed to pass through a filter of packed asbestos from the saturating apparatus in a simple gas-flow system. These experiments gave results so close to those given in Table IV and V that they are not repeated here. The agreement between the experiments indicates that no serious error has arisen from the experimental difficulties mentioned above.

TABLE IV.

Toxicity of vapours of contact insecticides to *Calandra granaria* and *Sitotroga cerealella.* (Percentage mortality after varying periods is shown.)

Insecticide vapour	Time of exposure (hr.)	*G. granaria*	*S. cerealella*
	2	0	0
p, p′ DDT ..	4	0	0
	8	0	0
	2	0	0
Commercial DDT	4	0	0
	8	100	100
	2	0	0
γ BHC ..	4	100	100
	8	100	100
	2	0	0
Controls (air only)	4	0	0
	8	0	0

Discussion.

The experiments reported above extend and confirm the results of Butterfield, Parkin & Gale (1949). Substantial vapour-phase activity of BHC, and of the volatile impurity commonly present in commercial DDT, undoubtedly occurs directly against infestations. By cumulative sorption on stored products a less transient protection can be acquired. Because this cumulative transfer is uncontrolled, the attendant dangers of taint from BHC, reduction of viability of seeds, and chronic toxicity to consumers of the stored products need to be considered in individual applications.

TABLE V.

Toxicity to eggs of *Tribolium confusum* and *Sitotroga cerealella* of some contact insecticide vapours. (Percentage of eggs hatching is shown.)

Insecticide	*T. confusum*	*S. cerealella*
p, p′ DDT ..	92, 90, 98, 86	100, 96, 68, 96
Commercial DDT ..	98, 98, 92, 96	94, 88, 96
γ BHC ..	96, 98, 90, 92	0, 0, 20, 0, 30, 0
Control ..	86, 92, 88, 100	98, 94, 100, 94, 90, 84

Butterfield & others (1949) indicate that in temperate climates whole wheat may safely be stored in bags impregnated with 5 per cent. DDT. A higher vapour-phase transfer is to be anticipated in tropical regions, but in practice, when full-sized bags are used, there would be a lower contamination, averaged over the whole sack, than was found in the smaller sacks used by Butterfield & others.

The fact that, for whole wheat exposed to DDT vapour, a new generation of *Calandra granaria* can survive within the endosperm, as can the developing *Sitotroga cerealella* larvae which are able to penetrate the seed coat, deserves special attention. It suggests that the DDT sorbed is strongly held by the seed coat. After milling this wheat, little DDT would be left in the flour, but the bran might be dangerously toxic. The strong sorption of other fumigants on the bran of wheat relative to the endosperm, has been shown for ethylene oxide, trichloroacetonitrile and methyl bromide by Lubatti & Harrison (1944) and is probably a widespread phenomenon.

Butterfield & others (*loc. cit.*) found that the transfer of DDT to groundnuts was greater than occurred with fat-free commodities. The experiments reported here, however, indicate that groundnuts so fumigated are less effectively toxic to insects than grain that has been similarly treated. An explanation of this apparent discrepancy may lie in the ability of the fat in the groundnuts to distribute the oil-soluble insecticide through the nut, whereas in grains the insecticide seems to be concentrated in the seed coat where, although smaller in quantity, it is more concentrated and more available to the insects infesting the commodity. The experiments reported here, although somewhat artificial by comparison with the conditions inside sacks impregnated with insecticides, suggest that the transfer of the p,p′DDT to stored products is of greater practical importance than the direct fumigating action of the insecticide. The distinction drawn in this paper between a direct fumigating action and the toxicity of sorbed fumigants will in practice become indistinct. Control of infested commodities in sacks sprayed with γ BHC will be associated with both vapour from the sacking and that desorbed from the stored products, and the relative importance of the two types of action is hard to assess. The ovicidal activity, for at least one species, which BHC vapour exerts may be useful when smoke generators are used to disinfest empty warehouses.

The results obtained with a commercial specimen of DDT strongly suggested that a volatile impurity was responsible for the enhanced toxicity of stored products exposed to its vapours, and the considerable direct fumigating action. Prolonged aspiration of a sample of commercial DDT for 48 hours renders negligible this direct action, and this fact further supports the suggestion that the enhanced toxicity is associated with an impurity which may prove to be p-dichlorobenzene, although no positive identification has been made.

The hazards of vapour-phase transfer of the insecticides have been investigated chemically by several workers, whose conclusions are summarised by Page & Blackith (1953). Generally, the total transfer to bagged commodities seems to be within the permitted limits during the periods for which storage in impregnated bags is likely.

Summary.

Both p,p′DDT and a sample of commercial DDT have been compared with γ BHC as insecticides acting in the vapour phase. Both the direct fumigant action of the insecticides and the toxicity of the vapours sorbed on to stored products have been examined. After storage in atmospheres saturated with the vapours for six months, wheat retained sufficient of all three insecticides to control adults of *Calandra granaria* (L.) and inhibit the development of larval *Sitotroga cerealella* (Ol.). This control and inhibition was complete for BHC, and stronger for commercial than for p,p′DDT. Similar results were obtained when the insecticides sorbed on flour were tested using the eggs or larvae of *Tribolium confusum* Duv., or when fumigated groundnut kernels were tested against *T. confusum*, but such groundnuts produced little toxic action against *Oryzaephilus surinamensis* (L.).

When the direct fumigant action of the vapour was examined, commercial DDT was found to have a rapid toxic action in the vapour phase against both *C. granaria* and *S. cerealella*. Since this toxicity was not found with p,p′DDT, there seems likely to be a toxic volatile impurity in commercial samples. This supposition was supported by the fact that commercial DDT subjected to prolonged aspiration did not give a pronounced fumigant effect. BHC had a more pronounced fumigant action than commercial DDT to both *Calandra* and *Sitotroga*, but perhaps the most interesting result with this insecticide was its ovicidal action against eggs of *Sitotroga*, although *Tribolium* eggs were not affected.

Acknowledgements.

The author is indebted to Professor J. W. Munro for permission to work in his laboratories during the tenure of a scholarship from the Government of Pakistan which is gratefully acknowledged. The author also wishes to thank Dr. A. B. P. Page under whose supervision the work was carried out and Dr. R. E. Blackith for his constructive criticism and advice and help in the preparation of the manuscript.

References.

Balson, E. W. (1947). Studies in vapour-pressure measurements. III. An effusion manometer sensitive to 5 × 10^{-6} mm. Hg. vapour pressure of DDT and other slightly volatile substances.—Trans. Faraday Soc., **43**, pp. 54–60.

Butterfield, D. E., Parkin, E. A. & Gale, M. M. (1949). The transfer of DDT to foodstuffs from impregnated sacking.—J. Soc. chem. Ind., Lond., **68,** pp. 310–313.

Davidson, G. & Burnett, G. F. (1952). Apparent fumigant action of non-volatile insecticides in African huts.—Nature, Lond., **170,** p. 893.

Hadaway, A. B. & Barlow, F. (1952). Sorption of insecticides by dried mud.—Nature, Lond., **167,** p. 854.

Lubatti, O. F. & Harrison, A. (1944). Determination of fumigants. XVII. Comparison of the sorption of hydrogen cyanide, ethylene oxide, trichloroacetonitrile, and methyl bromide by wheat.—J. Soc. chem. Ind., Lond., **63,** pp. 353–359.

Nasir, M. M. (1947). Eradication of insect pests of stored grains rather than their control.—Curr. Sci., **16,** pp. 10–13.

Page, A. B. P. & Blackith, R. E. (1953). Some non-agricultural uses of insecticides.—Rep. Progr. appl. Chem., **37,** pp. 27–37.

Wichmann, H. J., Patterson, W. I., Clifford, P. A., Klein, A. K. & Claborn, H. V. (1946). Decomposition and volatility of DDT and some of its derivatives.—J. Ass. off. agric. Chem. Wash., **29,** pp. 218–233.

STUDIES ON *STENOBRACON DEESAE* (CAM.), A PARASITE OF CERTAIN LEPIDOPTEROUS BORERS OF GRAMINACEOUS CROPS IN INDIA.

By E. S. Narayanan, M.A., Ph.D.(Lond.), D.I.C., F.R.E.S., F.E.S.I.
and
R. P. Chaudhuri, M.Sc., Ph.D.(Lond.), F.R.E.S.

Indian Agricultural Research Institute, New Delhi. E.H.N.

Stenobracon deesae (Cam.) parasitises several different species of Lepidopterous borers of sugar-cane (*Saccharum officinarum*), maize (*Zea mays*), jowar (*Sorghum vulgare*) and other crops in India. It is therefore of economic importance. It is an ectoparasite of the larva. Cameron (1902) described this insect first under the name *Bracon deesae*. Later, Ramakrishna Ayyar (1923, 1925, 1928), Husain (1936), Narayanan (1938), and Cherian & Israel (1938) reported its occurrence in different parts of India attacking a variety of insect pests. Most of these authors studied the taxonomy and morphology of the parasite, but Cherian & Israel gave a short account of its life-history and habits. In view of its possible value for biological control in the field, knowledge of its habits, fecundity and sex-ratio, and of the factors associated with oviposition and host selection by it and methods of rearing it in the laboratory is essential. Consequently, a number of experiments were conducted in the Parasite Laboratory of the Division of Entomology, Indian Agricultural Research Institute, during 1949–50. The results of these experiments are given in this paper.

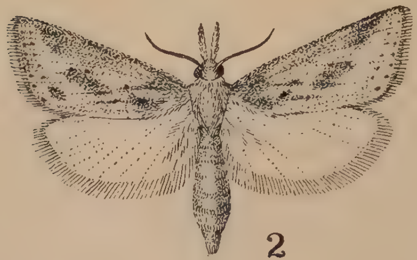
Method.

The adult parasite (fig. 1) was collected from sorghum and maize in the field where it attacks the larvae of *Chilo zonellus* (Swinh.) (fig. 2). In the laboratory, two different kinds of caterpillars were used as hosts, *Chilo zonellus*, obtained from sorghum in the field, and *Corcyra cephalonica* (Staint.), bred in the laboratory. For experimental oviposition by the parasite, the host larva was inserted artificially into a sugar-cane stem. A groove was made in the pith of a cane stem split longitudinally, a larva was placed in the groove and a piece of cellophane was fixed firmly over it (fig. 5). A fine hole leading into the groove was made through the stem so that the parasite could insert its ovipositor and reach the host (fig. 6). The parasite and host were kept in a glass rearing jar, the mouth of which was covered with thin muslin. Glucose solution (10 per cent.) on cotton-wool served as food for the adult parasite. Except where otherwise stated, male and female parasites were enclosed together in the jar for at least 24 hours so that they might pair before oviposition. Fully fed parasite larvae were transferred from the stems to short paper tubes for pupation.

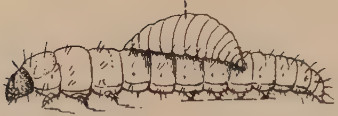
Experiments.

Oviposition.

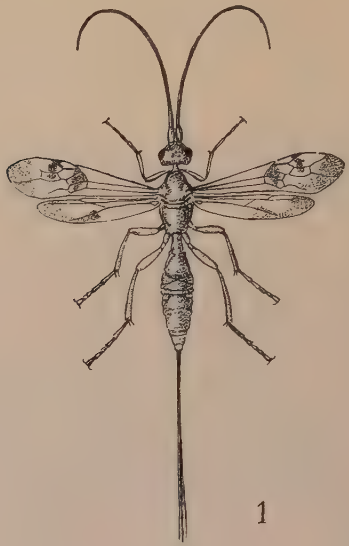
Experiments were conducted to ascertain whether the parasite would oviposit on hosts which were not inside plant tissues. In a number of cases, *Chilo* larvae were enclosed in rearing jars with parasites that had already started laying eggs. Although the insects were left thus for two to three days, no egg was laid on



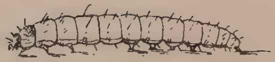
2



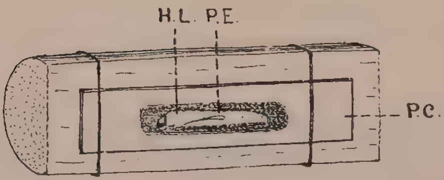
3



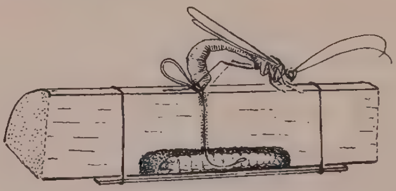
1



4



5



6

Fig. 1.—Adult female of *Stenobracon deesae* (Cam.), × 1·33.
Fig. 2.—Adult female of *Chilo zonellus* (Swinh.), × 1·33.
Fig. 3.—Fully grown larva of *Chilo* with a larva (P.L.) of *S. deesae* feeding on it, × 1·33.
Fig. 4.—Fully grown larva of *Corcyra cephalonica* (Staint.), × 1·33.
Fig. 5.—Portion of a sugar-cane stem slit longitudinally with a *Chilo* larva (H.L.) in its groove covered with a piece of cellophane (P.C.), × 0·66. The host larva (H.L.) bears an egg (P.E.) of the parasite, *S. deesae*.
Fig. 6.—Female of *S. deesae* laying an egg on a host larva by passing the ovipositor through the fine hole in the stem. Half of the portion of stem shown in fig. 5 is shown here, × 0·66.

any of the larvae, but later, when the same parasites were supplied with hosts inside plant stems they oviposited readily. These observations showed that in spite of the urge to oviposit, *S. deesae* does not lay eggs on larvae which are not inside stems. This necessitated the use of hosts inside cane stems in all the other experiments described here.

Observations showed that when ovipositing, the female parasite first determines the position of the fine hole in the cane stem containing the host by feeling with the antennae and, after moving to and fro on the stem for a little while, inserts the tip of its ovipositor into the hole, with the help of the third valvulae, bending the posterior abdominal portion at about a right angle to the body. After several attempts, the ovipositor is inserted completely into the stem and is thrust into the body of the host and withdrawn immediately; this is indicated by a jerk of its body. The ovipositor is then again inserted into the stem and an egg is laid on the body of the host larva. It appears that the host is paralysed before oviposition. The parasite larva does not feed on non-paralysed hosts, and the paralysis could not be caused by mechanical puncture. Immediately after hatching, the parasite larva begins to feed on the host by sucking its contents.

Superparasitism.

The phenomenon of superparasitism is an important factor in the usefulness of an insect parasite. It is equally important from the point of view of the study of insect behaviour and insect populations. The term superparasitism was first introduced by Fiske (1910) to denote the phenomenon that results " when any individual host is attacked by two or more species of primary parasites, or by one species more than once." Later, Smith (1916) restricted the meaning of this term to " that form of symbiosis occurring when there is a superabundance of parasites *of a single species* attacking an individual host insect." It is in this latter sense that the term is used in this paper. Fiske (*loc. cit.*) says that " the prevalence of superparasitism depends entirely upon whether or not the female parasite is gifted with a prescience which will enable her to select healthy hosts for her offspring." In order to study this phenomenon in the case of *S. deesae*, the following experiments were performed.

In the first series, six female parasites which had started egg-laying were provided with parasitised host larvae which had been attacked only 24 hours earlier and from which the parasite eggs had been removed. New parasitised hosts were supplied to each female at intervals of 24 hours until its death.

TABLE I.

Oviposition by *Stenobracon deesae* on parasitised hosts (*Chilo* larvae).

Serial No. of parasites	Time of exposure					
	1st day	2nd day	3rd day	4th day	5th day	6th day
1	2/1	0/1	2/1	1/1	D	
2	0/2	1/1	2/1	0/1	0/1	D
3	0/1	2/2	0/1	D		
4	2/1	1/2	0/1	D		
5	1/1	2/2	2/1	0/1	D	
6	1/1	1/1	2/1	0/1	D	

Numerator = No. of eggs.
Denominator = No. of hosts.
D = Death of parasite.

The results are given in Table I; on 14 occasions out of 23, the parasites laid eggs on parasitised hosts, and in a few cases two eggs were laid on one host. This experiment showed that either the female *S. deesae* is unable to distinguish parasitised from unparasitised hosts or its restraint against attacking parasitised hosts is limited.

In the next series of these experiments, both parasitised and unparasitised hosts were supplied together to a number of parasites. *Chilo* larvae that had been exposed to female parasites the preceding day were examined and those on which parasite eggs were found were put in fresh cane stems to use as parasitised hosts in this experiment. Both parasitised and unparasitised hosts were put at random in the same rearing jar on each occasion. The results are shown in Table II.

TABLE II.

Oviposition by *Stenobracon deesae* on parasitised and unparasitised hosts (*Chilo* larvae) exposed together.

Serial No. of experiment	No. of parasites	Duration of exposure	Eggs on parasitised hosts	Eggs on unparasitised hosts
1	7	24 hrs.	2/12	8/12
2	7	24 ,,	0/12	9/12
3	7	48 ,,	1/12	12/12
4	3	24 ,,	0/6	3/6
5	6	24 ,,	0/12	8/6
Total			3/54	40/48

Numerator = No. of eggs.
Denominator = No. of hosts.

Table II shows that if unparasitised hosts are available, *S. deesae* usually does not lay eggs on parasitised hosts. In these tests, 40 eggs were laid on 48 unparasitised hosts and only three eggs on 54 that were already parasitised. This indicates that the female *S. deesae* can discriminate between parasitised and unparasitised hosts and that oviposition on the former must be due either to error of judgment or to the breakdown, in the absence of sufficient suitable hosts, of the restraint against attacking parasitised individuals.

It has been suggested (*e.g.*, Chrystal, 1930; Salt, 1937) that the parasite of a burrowing host avoids superparasitism by recognising an oviposition canal that has been used previously and refraining from using it again. In order to test this in the case of *S. deesae*, the following experiment was performed. In each of the five experiments, one of the two lots of unparasitised hosts was placed in cane stems which had been used previously for oviposition and the other lot was placed inside fresh stems. A batch of parasitised hosts was put in fresh stems. All these hosts were exposed to parasites simultaneously in the same jar. The results are shown in Table III.

Table III shows that *S. deesae* lays more eggs on hosts inside already used stems (36 eggs on 34 hosts) than on those inside fresh (unused) stems (20 eggs on 32 hosts). This may mean that the parasite is enabled to locate the position of an oviposition canal by an odour which is emitted from it. Further, this experiment corroborates the preceding one in showing that if unparasitised hosts are available, *S. deesae* does not normally oviposit on parasitised ones. Only three eggs were laid on 46 parasitised hosts whereas 20 eggs were laid on 32 unparasitised hosts kept under similar conditions.

Although this experiment showed that *S. deesae* can distinguish parasitised from unparasitised hosts and normally favours the latter, superparasitism was not altogether absent. Experiments were therefore conducted to study the degree of superparasitism. In each experiment, healthy (unparasitised) *Chilo* larvae in fresh cane stems were put in a rearing jar into which some parasites were released, and after the desired period of exposure the hosts were examined and the number of parasite eggs found on each of them recorded. The details of the experiment and the results obtained are shown in Table IV.

TABLE III.

Oviposition by *Stenobracon deesae* on unparasitised hosts placed inside used and unused stems and parasitised hosts placed inside unused stems.

Serial No. of expt.	No. of parasites	Duration of exposure	No. of eggs on		
			Unparasitised hosts in used stems	Unparasitised hosts in unused stems	Parasitised hosts in unused stems
1	7	24 hrs.	8/5	3/6	1/12
2	7	24 ,,	8/8	4/6	1/10
3	7	24 ,,	8/7	4/6	0/10
4	6	24 ,,	5/6	3/6	0/6
5	8	72 ,,	7/8	6/8	1/8
Total			36/34	20/32	3/46

Numerator = No. of eggs.
Denominator = No. of hosts.

TABLE IV.

Number of eggs laid by *Stenobracon deesae* on individual hosts.

Expt.	No. of hosts	No. of parasites	Duration of exposure	No. of hosts bearing							Total eggs
				0 egg	1 egg	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	
1	2	6	24 hrs.	—	—	—	1	—	1	—	8
2	8	4	24 ,,	3	4	1	—	—	—	—	6
3	12	6	24 ,,	2	3	5	2	—	—	—	19
4	12	6	24 ,,	2	7	2	1	—	—	—	14
5	20	6	48 ,,	4	12	4	—	—	—	—	20
6	24	7	24 ,,	15	8	—	1	—	—	—	11
7	24	6	48 ,,	10	12	1	1	—	—	—	17
8	24	6	48 ,,	5	13	5	—	1	—	—	27

It is seen from Table IV that when in the first experiment six female parasites were supplied with only two hosts for 24 hours, five eggs were laid on one and three on the other, but in the second, when the number of hosts was greater than that of the parasites (eight hosts to four parasites), only one host had more than one egg (two eggs) laid on it. In each of the next two, when six parasites and 12 hosts were used, superparasitism occurred in a number of cases, but its intensity was not very high. The maximum number of eggs found on any one host was three only. The later experiments showed that when the number of hosts was increased to four times that of the parasites and the hosts were exposed to the parasites for 48 hours, few cases of superparasitism occurred and the greatest number of eggs found on any one host was four only.

However, in the experiment described above, it seemed probable that overcrowding of hosts and parasites in the experimental jar contributed to the superparasitism observed. Therefore, another series of similar experiments was performed in an attempt to eliminate this factor. In this series, only three female parasites and 12 hosts were placed on each occasion in each of two rearing jars of the same size as those used in the preceding experiment. The results of this experiment are shown in Table V.

TABLE V.

Number of eggs laid by *Stenobracon deesae* on individual hosts.

Expt.	Duration of exposure	Jar	No. of hosts bearing				Total eggs
			0 egg	1 egg	2 eggs	3 eggs	
1	48 hrs.	1st	5	5	2	—	9
	48 ,,	2nd	4	7	1	—	9
2	24 hrs.	1st	6	5	1	—	7
	24 ,,	2nd	7	5	—	—	5
3	24 hrs.	1st	9	2	1	—	4
	24 ,,	2nd	8	3	1	—	5

Table V shows that when the density of parasites and hosts is comparatively low, superparasitism is uncommon and even when it occurs the intensity is low. Out of 33 hosts that were attacked by parasites in this experiment, superparasitism occurred in only six cases and the greatest number of eggs laid on one host was two only.

It has been found that when more than one egg is laid by a female of

TABLE VI.

Life-cycle of *Stenobracon deesae* in different periods of the year.

	Stage	No. of observations	Average duration (days)	Minimum duration (days)	Maximum duration (days)
A. December–March; in incubator at 26°C. and 75% R.H.	Egg	230	1·11	1	2
	Larval	163	5·4	3	11
	Pupal	138	16·8	10	31
	Total		23·31		
B. June–July; in laboratory (temp.– max. 102°F.; min. 82°F.: R.H.–max. 99%; min. 25%)	Egg	188	1	1	1
	Larval	128	2·7	2	4
	Pupal	104	10·4	7	14
	Total		14·1		
C. November–December; in laboratory (temp.– max. 73°F.; min. 57°F.: R.H.–max. 49%; min. 14%)	Egg	53	2	1	4
	Larval	28	10·6	6	17
	Pupal	23	31·1	16	45
	Total		43·7		

S. deesae upon a single host, all may hatch but the resulting larvae feed upon one another and only one survives to pupate. They feed upon their own kind even when the host is available. On several occasions 2–5 eggs or larvae of the parasite were kept together with or without a host and in all cases only one parasite survived. A point of economic importance in this connection is that as the struggle among the parasite larvae occurs very early, before the normal food supply is exhausted, the survivor does not suffer from undernourishment or starvation.

Life-cycle.

The durations of the different stages of the life-cycle vary greatly according to the physical conditions of the surroundings. Table VI shows that at a temperature of about 26°C. and a relative humidity of 75 per cent., the average duration of the life-cycle is 23·31 days. Under laboratory conditions in June and July, when the temperature was high and the humidity often low, the parasite developed quickly, the whole life-cycle being completed on the average in only 14·1 days. During the cold and dry days of November and December, however, the average duration of the life-cycle was 43·7 days in the laboratory. Cherian & Israel (1938) found the egg, larval and pupal periods to be 23–31 hours, 3–6 days and 5–8 days, respectively, under the conditions prevailing in Coimbatore, southern India, whereas Narayanan (1938) recorded a period of 22–25 days for the larval stage under conditions at Pusa (Bihar).

Duration of life of the adult.

In the period June–December 1949 the adult life of 39 females reared from *Chilo* larvae varied in duration from 10 to 83 days, the average being 29·5 days. The corresponding figures for 27 females reared on *Corcyra* larvae in the period July 1949 to February 1950 are 18 to 98 days and 44·8 days.

Except during the very cold months (December to February), the parasites were reared under ordinary laboratory conditions. During December–February, they were kept in an incubator in which constant conditions of about 26°C. and 75 per cent. relative humidity were maintained. The average adult life of 66 females in June–February was 35·7 days. Ten female parasites were reared during the cold months under ordinary laboratory room conditions, two of these lived 107–122 days but laid only five and seven eggs, respectively, oviposition not having started until they were 100 days old; although the other eight lived for 80–128 days they did not oviposit, whereas their contemporaries in the incubator did so. The duration of life of 160 males reared in October–May averaged 42·7 days.

These observations indicate that *S. deesae* may pass the winter hibernating as an adult and that a stock of parasites could be maintained in the laboratory throughout the year. Under conditions at Delhi, the parasite first appears on maize and sugar-cane in the field in the middle of April and it is seen up to the end of November on sorghum. In all these crops, the host is *Chilo zonellus*.

Fecundity.

The average number of eggs laid per female was found to be 23·76 among 68 females for which separate records were kept (Tables VII A and VII B). The maximum number of eggs laid by a single female was 58. Usually, when a parasite died after having apparently completed egg-laying, it was dissected, but in no case was a single mature egg found in the ovaries. It will be seen from Tables VII A and VII B that only about one-third of the eggs laid yielded adults. Whether this applies in the field is not known.

Tables VII A and VII B show that although *Corcyra* is not a natural host of this parasite, the mortality in the different stages of development of the parasite was only slightly higher when the host was *Corcyra* than when it was *Chilo*.

Sex-ratio.

The ratio of males to females in 227 *S. deesae* collected from jowar fields was about 3:1. In the laboratory, of the 350 individuals reared on *Chilo* larvae, 71·2 per cent. were male (Table VII A), but of the 213 reared on *Corcyra* larvae,

TABLE VIIA.

Progeny produced with *Chilo* larvae as hosts.

Serial No. of parent parasite	No. of eggs laid	No. of larvae produced	No. of pupae produced	No. of adults		
				Males	Females	Total
		From 15.vi.49 to 21.viii.49				
1	14	13	6	4	2	6
2	9	8	7	4	1	5
3	19	16	12	2	2	4
4	24	21	16	10	3	13
5	19	15	10	6	3	9
6	20	17	13	7	4	11
7	23	20	14	7	6	13
8	17	14	12	7	2	9
9	26	24	18	8	3	11
10	11	10	7	3	1	4
11	13	10	8	5	1	6
12	13	9	7	3	1	4
13	8	6	5	3	1	4
14	12	9	5	2	1	3
15	29	26	23	17	0	17
		From 4.viii.49 to 27.ix.49				
16	58	47	37	6	8	14
17	34	27	21	9	1	10
18	37	28	24	3	10	13
19	42	35	24	14	0	14
20	30	26	18	7	4	11
21	16	14	22	7	0	7
22	38	25	19	7	4	11
23	29	23	18	6	0	6
24	31	24	18	8	0	8
		From 8.ix.49 to 4.i.50				
25	11	7	5	3	0	3
26	26	21	17	7	3	10
27	13	11	6	4	0	4
28	34	24	15	7	4	11
29	58	42	25	15	5	20
30	12	9	7	4	1	5
31	21	17	12	2	9	11
32	15	12	5	2	1	3
33	41	30	20	15	1	16
34	48	37	18	6	6	12
35	25	18	9	5	2	7
36	56	45	22	8	11	19
37	15	14	11	9	0	9
38	22	10	4	2	0	2
39	8	8	5	5	0	5
Total 39	977	772	545	249	101	350
Average	25·05	19·7	13·9	6·3 or 71·2%	2·5 or 28·8%	8·9

93·8 per cent. were male (Table VII B). The *Corcyra* larva is not a natural host of *S. deesae* and is much smaller than the *Chilo* larva (see figs. 3 & 4); the weight of a *Corcyra* larva is only about one-third of that of a *Chilo* larva. However, in the breeding experiments described above, each parasite larva was usually supplied with more than one *Corcyra* larva, so that the possibility of the parasites being starved or undernourished did not arise. This result shows that the sex-ratio of *S. deesae* may vary according to the host species, and indicates that males always predominate. The reason why the sex-ratio of a parasitic insect varies according to the host is still not clearly understood, but is discussed below in the light of our experimental results. Here, it is sufficient to point out that although *Corcyra* is easy to breed in bulk in the laboratory, the unfavourable sex-ratio of *S. deesae* which results from its use as host for this parasite

TABLE VIIB.

Progeny produced with *Corcyra* larvae as hosts.

Serial No. of parent parasite	No. of eggs laid	No. of larvae produced	No. of pupae produced	No. of adults		
				Males	Females	Total
		From 18.vii.49 to 16.viii.49				
1	11	8	7	3	0	3
2	27	22	14	9	0	9
3	33	28	21	9	2	11
4	14	12	8	5	0	5
5	13	10	5	3	1	4
6	13	12	7	3	0	3
7	14	12	9	5	0	5
8	28	22	15	9	1	10
9	26	16	10	5	0	5
10	17	15	10	5	0	5
11	35	24	17	9	0	9
12	48	30	24	9	1	10
13	28	23	15	7	1	8
14	18	16	15	7	0	7
		From 6.ix.49 to 30.ix.49				
15	17	11	7	2	0	2
16	16	10	6	2	0	2
		From 3.xii.49 to 24.iv.50				
17	6	5	5	5	0	5
18	20	14	12	8	1	9
19	35	27	20	12	0	12
20	33	26	17	14	1	15
21	27	21	10	7	0	7
22	34	27	20	19	0	19
23	12	8	4	3	0	3
24	5	4	4	4	0	4
25	19	14	11	8	0	8
26	23	18	10	8	0	8
27	32	23	17	9	2	11
28	12	8	7	5	0	5
29	23	20	16	6	3	9
Total 29	639	486	343	200	13	213
Average	22·03	16·7	11·8	6·8 or 93·8%	0·4 or 6·2%	7·3

renders it unsuitable for use in connection with the bulk-breeding of the parasite for biological control.

The progeny of virgin *S. deesae* were always found to be males.

Discussion.

It is evident from the results of these investigations that *S. deesae* can distinguish unparasitised hosts from those that are parasitised and that if ample healthy hosts are available it avoids laying eggs on those already parasitised. However, when only parasitised hosts are available or the number of hosts is very limited, parasitised hosts are attacked; evidently the normal reluctance of the parasite to oviposit on parasitised hosts breaks down in these circumstances. These observations corroborate those made by Salt (1934) on *Trichogramma evanescens* Westw. It is interesting to consider how *S. deesae* discriminates between parasitised and unparasitised hosts. The host remains inside the plant tissues where it is not possible for the parasite to use its sense of taste or smell by means of its antennae as has been suggested for *Trichogramma* (Salt, 1937). Furthermore, neither the tactile organs situated upon the tarsi nor the sensitive tip of the abdomen believed by Ullyett (1936) to be used by *Microplectron* seem to be of use in this connection in *Stenobracon*. The only possible way it can judge the quality of the host seems to be by means of its ovipositor. It is probable that when a female *Stenobracon* inserts its ovipositor into a host to paralyse it before oviposition, she receives a stimulus from a healthy host which is different from that derived from a parasitised host. The stimulus may even be different in different species of hosts. Salt (1934) says that *Collyria calcitrator* (Grav.) and *Ibalia leucospoides* (Hochenw.), which also parasitise hosts that live inside plant tissues, can distinguish between healthy and parasitised hosts. In each of these cases, as in *S. deesae*, only the ovipositor of the parasite can reach the host. The same author (Salt, 1937) quotes Chrystal (1930): "*Ibalia*, once she has used an oviposition tunnel, frequently crosses and recrosses it seeking for other tunnels in which to oviposit. It is probable, therefore, that she recognizes those tunnels which she has already visited and possibly she leaves some odour behind her by which other females are also furnished with this information." Agreeing with this view, Salt (1937) concludes that: "This suggestion is given weight by the result now obtained with *Trichogramma*. Henceforth, when a parasite of a burrowing host is found to avoid superparasitism the occurrence of a chemical trace on the surface of the plant is at once to be suspected." The result of our experiment given in Table III does not, however, confirm this generalisation. In the case of *S. deesae*, an odour may be left on the tunnel at the time of oviposition but that odour does not seem to prevent superparasitism. In our experiments, when healthy hosts were placed inside already used and unused cane stems, more eggs were laid through those oviposition tunnels that had been used before than through the fresh tunnels. This suggests that the chemical trace left on the oviposition tunnels, instead of deterring the parasite, actually encourages it to use the same tunnels again, and that it is only when the ovipositor penetrates into the hosts that the parasite can distinguish between parasitised and healthy hosts and can thus largely avoid superparasitism.

Another point of special interest is the difference in sex-ratio of *S. deesae* bred on *Chilo* and *Corcyra* larvae. Several investigators have paid attention to the sex-ratio of parasitic insects and the influence of host species on it. One of the important factors influencing the sex-ratio in parasites is the size of the host. Chewyreuv (1913; *vide* Clausen, 1939) found that the great majority of individuals of *Pimpla* from large hosts were females whereas those from small hosts were predominantly males. Since that time, several other workers have noticed this fact in a number of other parasites, and it is now generally believed that the sex-ratio is largely controlled by the size of the individual hosts. The larger hosts tend to produce more females and the smaller hosts more males. Reasons that have been suggested for this by various workers are: (1) differential mortality of the sexes before completion of development, (2) a quantitative nutritional effect that determines the sex, and (3) selective oviposition by the female parent. In our experiments, when *S. deesae* was bred on its natural host, *Chilo*, the proportion of females was much higher than when *Corcyra* was the host; although it is true that the *Corcyra* larva is much smaller than the *Chilo* larva, this disparity in the sex-ratios could hardly be due to differential mortality of the sexes, because the average numbers of adult parasites reared on the two hosts were almost the same. Holdaway & Smith (1932), studying the sex-ratio of the Braconid parasite, *Alysia manducator* (Panz.), bred on hosts of different sizes, believed that the quantity of food as regulated by the size of the host played a part in determining the sex of the parasite, but this explanation cannot be applied to the present case, for when *Corcyra* was used as the host, nearly every parasite larva was supplied with more than one host larva so that the quantity of food supplied to each individual would be approximately equal to a *Chilo* larva.

Chewyreuv (*loc. cit.*) believes that the female parasite is able to deposit fertilised and unfertilised eggs at will and that those destined to produce females are laid on larger hosts. Similar views have been put forward by Brunson (1937) in his studies on the relation between the larval instars of *Popillia japonica* Newm. and the sex of its parasite, *Tiphia popilliavora* Roh. He found that when eggs of the parasite deposited on second-instar larvae were transferred to third-instar larvae for hatching and further development, the sex-ratio of the resulting adults did not differ much from that which would have been obtained if development had been completed on the second-instar hosts. Similarly, no change in the sex-ratio was obtained by transferring parasite eggs laid on third-instar hosts to second-instar hosts for development. He therefore believes that the female parasite has the ability to control the sex of her progeny at the time of oviposition and that "the stimulus to which the female responds in controlling the sex of her progeny is definitely associated with the instar or size of host on which the eggs are placed." Flanders (1939) says that "it is evident as suggested by Schrader (1920) in regard to the arrhenotokous aleyrodid (*Trialeurodes vaporariorum*) that the female fertilizes its eggs in response to a stimulus. The stimulation of the spermatheca probably results from the contact of the antennae, legs or ovipositor with the medium on which eggs are to be deposited. Variations in the condition of this medium may vary the amount of stimulation and it is probable that the spermatheca responds only to stimuli of certain intensity, reacting to its fullest extent or not at all. Such reflex appears to be responsible for the proportion of sexes in many Hymenoptera."

It is not possible to explain definitely the differences in sex-ratio observed in *S. deesae* when bred on two different hosts. We have as yet no knowledge of the anatomy of the spermatheca and associated organs, nor do we know whether the male is produced by both haploid and diploid eggs or by haploid only. However, in the light of our findings, it appears most likely that the sex of the progeny of *S. deesae* is controlled by the stimuli caused by the host at the time of oviposition in the way suggested by Flanders. The female *S. deesae* does not seem to distinguish between *Chilo* and *Corcyra* larvae, both of which are inside the plant tissues, by shape, as the Chalcid, *Microplectron*, is believed to distinguish its hosts (Ullyett, 1936), or by size as in the case of *Trichogramma evanescens* (Salt, 1935) or by smell with the antennae or legs, as suggested by Salt (1937) as the means by which *Trichogramma* distinguishes between parasitised and healthy hosts. Therefore the parasite probably distinguishes between its hosts by means of its ovipositor.

Summary.

Experiments were conducted to investigate oviposition and host selection by *Stenobracon deesae* (Cam.), a Braconid parasite of certain Lepidopterous borers of sugar-cane, maize and sorghum in India. The fecundity and sex-ratio of this parasite and the duration of its life-cycle were also studied.

Chilo zonellus (Swinh.) and *Corcyra cephalonica* (Staint.) were used as hosts. The former is one of the principal hosts in the field, but the latter is not normally a host of this parasite.

The female *Stenobracon* normally avoids laying eggs on hosts that are already parasitised by its own kind when unparasitised hosts are available; but in the absence of healthy hosts or when these are too crowded, parasitised hosts are attacked by it.

At a temperature of 26°C. and relative humidity of 75 per cent., the life-cycle of the parasite was completed, on an average, in 23·3 days, but under laboratory conditions at Delhi it took 14·1 days in June–July and 43·7 days in November–December. The average duration of adult life of females in June–February, mainly in ordinary laboratory conditions, was 35·7 days, and single females lived as long as 122 and 128 days. The adult male lived for 42·7 days on the average.

In the laboratory, the female lays about 24 eggs on an average, but only about one-third of them yield adults.

Males predominate. The sex-ratio appears to vary according to the host; among adults reared on *Chilo* larvae, 28·8 per cent. were females, but among others reared on *Corcyra* larvae, only 6·2 per cent. were females.

The phenomena of discrimination between parasitised and unparasitised hosts and of the change of sex-ratio with change of host are discussed. It is suggested that the ovipositor enables the parasite to recognise the host and that the stimuli received by the ovipositor from the host influence the functioning of the spermatheca which in turn controls fertilisation and finally the sex of the progeny.

References.

Brunson, M. H. (1937). The influence of the instars of host larvae on the sex of the progeny of *Tiphia popilliavora* Roh.—Science, **86**, p. 197.

Cameron, P. (1902). Descriptions of new genera and species of Hymenoptera collected by Major C. G. Nurse at Deesa, Simla and Ferozepore. Part II.—J. Bombay nat. Hist. Soc., **14**, pp. 419–449.

Cherian, M. C. & Israel, P. (1938). *Stenobracon deesae*, Cam. (Hym. Brac.) a natural enemy of the moth borers of sugarcane.—Madras agric. J., **26**, pp. 207–213.

* Chewyreuv [Shevyrev], I. (1913). Le rôle des femelles dans la détermination du sexe de leur descendance dans le groupe des Ichneumonides.—C.R. Soc. Biol., **74**, pp. 695–699.

* Chrystal, R. N. (1930). Studies of the *Sirex* parasites . . . —Oxf. For. Mem., no. 11, 63 pp.

Clausen, C. P. (1939). The effect of host size upon the sex ratio of Hymenopterous parasites and its relation to methods of rearing and colonization. —J. N.Y. ent. Soc., **47**, pp. 1–9.

Fiske, W. F. (1910). Superparasitism: an important factor in the natural control of insects.—J. econ. Ent., **3**, pp. 88–97.

---

* Originals not seen.

FLANDERS, S. E. (1939). Environmental control of sex in Hymenopterous insects.—Ann. ent. Soc. Amer., **32**, pp. 11–26.

HOLDAWAY, F. G. & SMITH, H. F. (1932). A relation between size of host puparia and sex ratio of *Alysia manducator* Panzer.—Aust. J. exp. Biol. med. Sci., **10**, pp. 247–259.

HUSAIN, M. A. (1936). Summary of the more important experimental results obtained by the Entomologist to Government, Punjab, Lyallpur during the years 1931–35.—Summ. Res. agric. Stas Res. Offrs Punjab 1930–35, pp. 169–182. (Rev. appl. Ent., (A) **25**, p. 45.)

NARAYANAN, E. S. (1938). A note on *Stenobracon deesae* (Cam.), a new parasite of the root-borer of sugarcane.—Indian J. agric. Sci., **8**, pp. 215–216.

RAMAKRISHNA AYYAR, T. V. (1923). Short notes on some South Indian insects.—Proc. 5th ent. Mtg Pusa, pp. 263–269.

RAMAKRISHNA AYYAR, T. V. (1925). Notes on the status of some parasitic Hymenoptera in South India.—J. Bombay nat. Hist. Soc., **30**, pp. 487–491.

RAMAKRISHNA AYYAR, T. V. (1928). A contribution to our knowledge of South Indian Braconidae. Part I. Vipioninae.—Mem. Dep. Agric. India (Ent. Ser.), **10**, pp. 29–60f.

SALT, G. (1934). Experimental studies in insect parasitism. II. Superparasitism.—Proc. roy. Soc. Lond., (B) **114**, pp. 455–476.

SALT, G. (1935). Experimental studies in insect parasitism. III. Host selection.—Proc. roy. Soc. Lond., (B) **117**, pp. 413–435.

SALT, G. (1937). The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts.—Proc. roy. Soc. Lond., (B) **122**, pp. 57–75.

SCHRADER, F. (1920). Sex determination in the white-fly (*Trialeurodes vaporariorum*).—J. Morph., **34**, pp. 267–298.

SMITH. H. S. (1916). An attempt to redefine the host relationships exhibited by entomophagous insects.—J. econ. Ent., **9**, pp. 477–486.

ULLYETT, G. C. (1936). Host selection by *Microplectron fuscipennis* Zett. (Chalcididae, Hymenoptera).—Proc. roy. Soc. Lond., (B) **120**, pp. 253–291.

THE BIOLOGY OF RED BOLLWORM, *DIPAROPSIS WATERSI* (ROTHS.) IN NORTHERN NIGERIA.

By Q. A. Geering.
Empire Cotton Growing Corporation, Cotton Research Station, Namulonge, Uganda,
and
A. F. H. Baillie.
*Plant Protection, Ltd., Fernhurst, Sussex.**

E.M.N.

(Plate XLIII.)

The red bollworm which attacks cotton in various parts of Africa was known for many years as *Diparopsis castanea* Hmps. Recently, however, Clements (1951) revised the genus *Diparopsis* and showed that the name *castanea* should be restricted to a species attacking cotton south of the equator, and that the one attacking cotton north of the equator, including Nigeria, is in fact a distinct species which he named *D. perditor*. It has subsequently been pointed out that an earlier name exists for this species (Pearson, 1954) and that it should be known as *Diparopsis watersi* (Roths.). All references to *Diparopsis* in Nigeria prior to 1951 give the then accepted name of *D. castanea*.

Early Work in southern Nigeria and the Discovery and Definition of the Problem in northern Nigeria.

The published observations on cotton pests, including red bollworm, in Nigeria relate mainly to the south, particularly to Ibadan in Oyo Province, where at the time attempts were being made to establish an exportable crop of cotton (Golding, 1928, 1929; Golding & others, 1927; Lean, 1927; Pomeroy, 1925; Pomeroy & Lean, 1925). Some of the later observations were made at Ilorin which, though included within the political division of the Northern Provinces, is at the extreme south of that area and belongs, climatically and agriculturally, to a middle zone, ecologically intermediate between the extreme northern and southern zones, but more similar to the latter (see fig. 1).

Eventually the attempt to grow an exportable cotton crop in the south was abandoned for a number of reasons, and the exportable crop is now produced entirely in the northern zone. The variety grown is a derivative of the American Upland variety, Allen, first introduced in 1912. In 1926 the Empire Cotton Growing Corporation established a seed farm at Daudawa in order to supply improved seed for the peasants, and at the same time to help increase total production. Reports from this farm from 1927–1939 frequently referred to damage by insect pests, notably "Sudan bollworm" (*Diparopsis*) and stainers (*Dysdercus* spp.); their incidence was not, however, considered serious. Yields of cotton were nevertheless low, and 320 lb. per acre of seed cotton was considered a good yield. Throughout this period, breeding and selection work was being carried out by officers of the Department of Agriculture at its Northern Provinces' headquarters at Samaru, near Zaria, 60 miles south-east of Daudawa (fig. 1). No entomologist had been stationed in this area, however, and it was not until

---

* Formerly with Empire Cotton Growing Corporation.

1947, when Mr. E. O. Pearson, then Senior Entomologist of the Empire Cotton Growing Corporation, visited Nigeria, that the insects attacking cotton in the north were critically examined in any detail. As a result of the report and recommendations following that visit (Hutchinson & Pearson, unpublished), detailed investigations were begun at Samaru in 1948.

In this report, Pearson referred to *Diparopsis*, *Earias* spp., *Platyedra gossypiella*, *Argyroploce leucotreta*, and *Dysdercus superstitiosus*, occurring throughout the northern cotton belt, and recommended investigation of their status and of means for reducing losses due to their activity. Particular attention was to be paid to *Diparopsis*, *Platyedra* and *Dysdercus*. The interest in *Platyedra* lay in the fact that its presence in Nigeria had only been discovered in 1944 (Golding, 1945). The present paper describes that part of the investigations concerned with the biology of *Diparopsis*, undertaken during the seasons 1948–51. The results have previously been reported in summary (Geering, 1950, 1951; Baillie & Geering, 1952). The relevant parts of these are now brought together and considered in detail. The economic status of *Diparopsis* and all other cotton insects will be considered in a later communication.

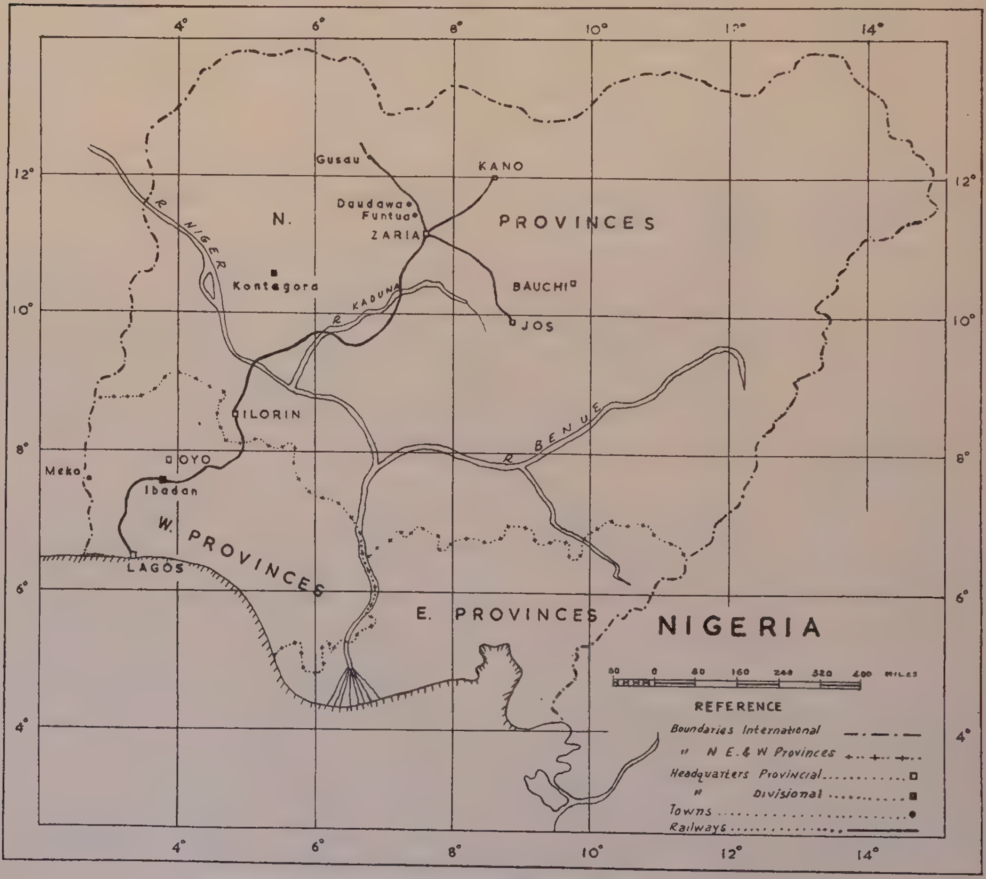

4°
6°
8°
10°
12°
14°
12°
10°
8°
6°
4°
Gusau
KANO
Daudawa
Funtua
ZARIA
N.
PROVINCES
R. NIGER
Kontagora
BAUCHI
R. KADUNA
JOS
ILORIN
R. BENUE
OYO
Meko
Ibadan
W. PROVINCES
LAGOS
E. PROVINCES
NIGERIA
80 0 80 160 240 320 400 MILES
REFERENCE
Boundaries International
" N E. & W. Provinces
Headquarters Provincial
" Divisional
Towns
Railways

Fig. 1.—Map of Nigeria, showing places mentioned in the text.

Climatic and Agricultural Conditions of the northern Cotton Belt.

The northern cotton zone falls within Latitudes 10–12°N. and this region experiences a single monsoon rainy season, which lasts from late March to early October. The rains are preceded during March by the onset of the south-west monsoon wind, accompanied by rises in temperature and humidity; intermittent falls of rain occur at the end of March. As the season progresses, the rainfall increases, and the humidity continues to rise, but temperatures fall. Fig. 2 shows the weekly total rainfall, and weekly mean percentage relative humidity recorded at Samaru during 1949, the season when the major aspects of the biology of *Diparopsis* were defined. The total rainfall for the season was 38·93 in. compared with the previous 25 years' average of 44·12 in. August is the wettest month, and in 1949 the total rainfall for that month was exceptionally high, *viz.*, 16·39 in., and over the 40-day period 4th August to 12th September a total of 21·3 in. of rain was recorded. Throughout this period waterlogging of the soil occurred, and soil temperatures were at a minimum (fig. 3). The abrupt change to dry-season conditions from the end of October is apparent in fig. 2. No rain normally falls between mid-October and the

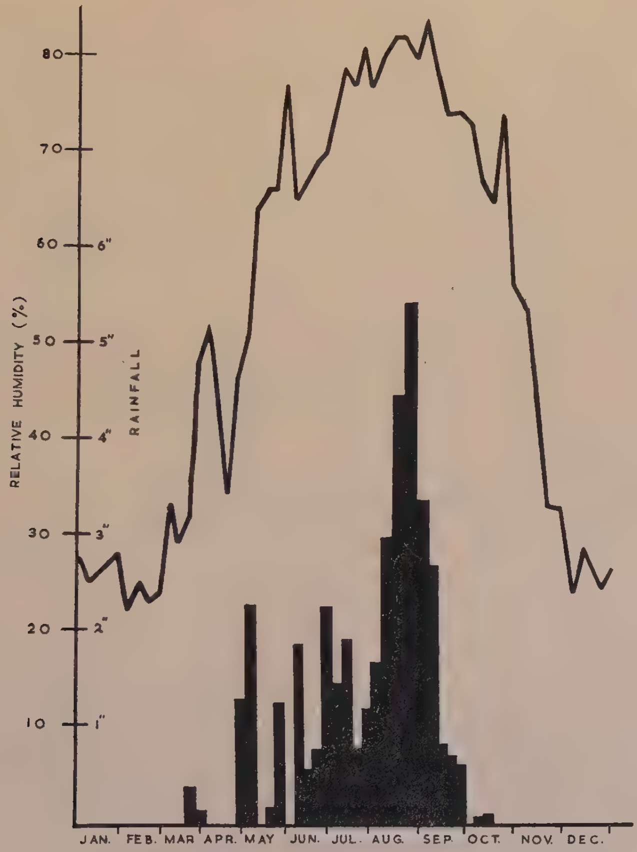


Fig. 2.—Weekly total rainfall and weekly mean relative humidity (mean of 8 a.m. and 2 p.m. readings), Samaru, 1949.

following March; during this period a drying north-east monsoon wind, the "Harmattan", blows from the Sahara, and the dry season is characterised by a wide diurnal range of temperature (fig. 6), and progressively lowering humidity. During late January and early February the midday relative humidity may drop to 5 per cent.

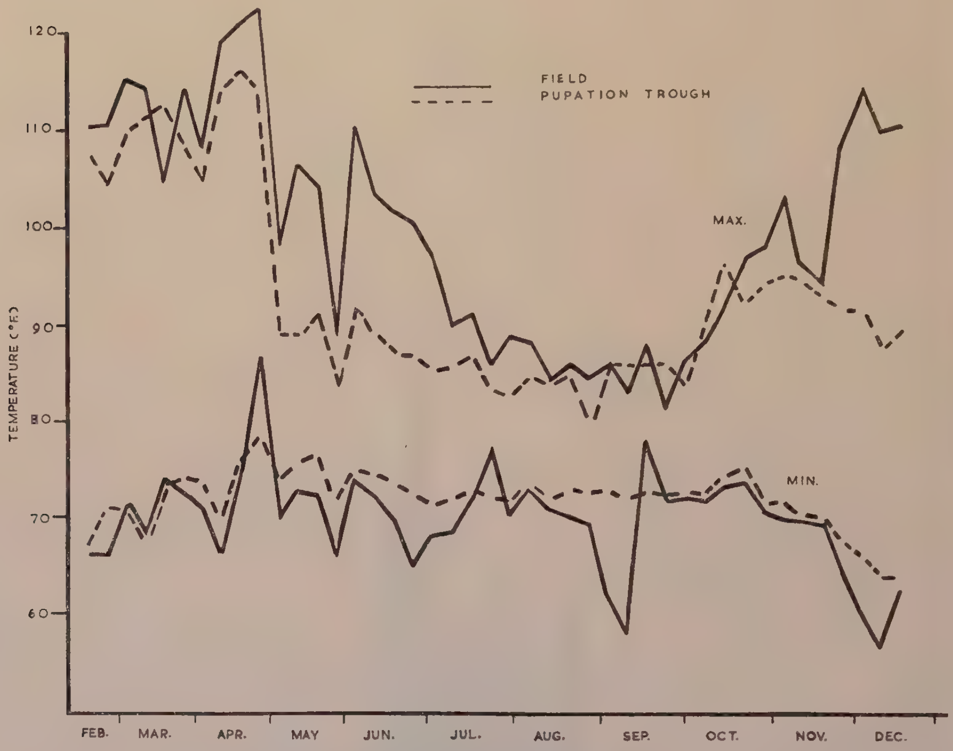


Fig. 3.—Weekly mean maximum and minimum soil temperatures at depth of 1½ inches, Samaru, 1949.

Under this climatic régime the agricultural system is based on grain crops, *viz.*, sorghum and bulrush millet, rotated with either of the two principal cash crops, groundnuts and cotton, the former being grown mainly in the northern part of the cotton belt or outside it on the lighter, sandier soils, and in areas with lower rainfall. The grain crops are sown in May, and only when adequate provision of food has been ensured is land prepared for the cash crops. This means that sowing of cotton rarely occurs earlier than July, and extends into August or even September, the latest sowings being made on freshly opened land. Peasant holdings are small, averaging 10 acres, and cultivation is continued for 4–6 years, followed by up to six years bush fallow.

In the more heavily populated areas around the larger villages and towns, although individual holdings may be small and scattered, the cotton plots are contiguous, and continuous areas of cotton may cover 20–30 acres. Elsewhere individual holdings will be separated by patches of bush fallow, and continuous areas of cotton larger than one acre are rare.

Previous Work on the Life-cycle of *Diparopsis*.

When the work in Nigeria was planned, it was believed that *castanea* was the only species of *Diparopsis* attacking cotton in Africa. A very full account of the life-history and annual cycle of activity of this species in the Lower River districts of Nyasaland has been published (Pearson & Mitchell, 1945*b*). The approach adopted in Nigeria was therefore planned on the lines of that used in Nyasaland and a brief résumé of the behaviour of *Diparopsis castanea* there will facilitate a description of the work in Nigeria.

Nyasaland lies between Latitudes 10° and 17°30′S., and the rainfall pattern at Port Herald on the lower Shire River (Lat. 17°S.) is similar to the northern cotton area of Nigeria, although the dry season is less severe. The main rains extend from December to April, with some early storms in November and light showers occasionally in June; the average rainfall recorded over 43 years in each of the months July to October is less than one inch.

At the time described the cotton crop was sown during the latter half of January and early February, and red-bollworm activity commenced in March and April, when moths emerged from diapause pupae produced in the preceding season. "Short-term" generations then followed each other at intervals of 5–6 weeks, depending on temperature, and the infestation reached a peak in May and June. The populations then declined, largely due to successive generations producing increasing proportions of diapause pupae. It was found that the conditions associated with the induction of diapause were characterised by wide diurnal ranges of temperature, together with low minima; and the character of the pupal period was predetermined, either in the larval stage or earlier. In Nyasaland, emergence from these diapause pupae extended from December to May, and was continuous, although there was a distinct drop in emergence during January, the wettest month in this region.

The main object of the investigation in northern Nigeria was to determine the annual cycle of activity of *Diparopsis*. With this information it would be possible to see whether by adjustment of the sowing date, or other measures, the main attack could be avoided. In Nyasaland, one of the alternative control measures proposed by Pearson & Mitchell was early sowing, in December, followed by early uprooting, in July. The object of this was to limit the production of diapause pupae, which were mostly formed from July onwards, *i.e.*, in the later part of the season. This has since been successfully carried out with subsequent reduction of red-bollworm damage. Accordingly, the following programme of investigations was initiated at Samaru and Daudawa in the Northern Provinces of Nigeria:—

(1) Standard plots of cotton were sown in early July (the normal date for commencing sowing) and the populations of red-bollworm eggs and larvae followed.

(2) Throughout the season, fully grown larvae were collected and allowed to pupate in cages in soil, and the emergence of moths recorded.

(3) Repetition of (1) using standover and ratoon cotton, to record the earliest commencement of activity.

(4) When information on the main pattern of activity had thus been obtained, a date-of-sowing trial was laid down to see whether red-bollworm attack could be avoided or reduced, and if so whether any advantage in yield resulted.

Items (1) to (3) were repeated, starting in 1949, at Gusau, in the extreme north, and at Kontagora, at the extreme south of the cotton belt. In the event, only records obtained under close supervision at Samaru and Daudawa yielded reliable detailed information, although a general picture of the pattern of activity at the other two stations was obtained.

General Pattern of Activity of *Diparopsis* in northern Nigeria.

Egg-laying.

Cotton sown in early July bore squares, *i.e.*, young flower buds, by the middle of August, and commenced flowering in early September. The early instars of red bollworm feed mainly on squares, but the later stages attack bolls. July-sown cotton is therefore liable to attack from the middle of August onwards. The patterns of egg-laying in such cotton at Samaru for the three seasons 1948–50 are shown in fig. 4. The records were obtained as follows. One-acre plots were sown with cotton on ridges three feet apart, with 2-foot spacing along the ridges, and two plants per stand. When the plants were four weeks old, 20 positions were marked at random, and on these plants eggs were counted twice each week, and at the same time removed from the plants. In this way, the total numbers of eggs laid per week were computed. In order to avoid abnormality in growth, caused by the handling of the plants and the inevitable treading of the ground during counting, the sampling positions were moved two positions along the ridge every four weeks. The considerable variability of the pattern of egg-laying is demonstrated by fig. 4, but this also shows that oviposition was at its peak in October and November, although it commenced in September and continued at a low level into December.

The highest level of egg-laying recorded at Samaru was in 1949, when two peaks of over 9,000 eggs per acre per week were recorded in October and November. These figures are very much lower than those recorded by Pearson & Mitchell in Nyasaland, where the peak of egg-laying in April and May was always from 15,000–20,000 per acre per week, and for at least two months was sustained at over 10,000 per acre per week. The only occasion when egg-laying of similar intensity occurred in Nigeria was at Daudawa in 1950, when two peaks of 12,000 and 20,000 eggs per acre per week were recorded, in September and early November, respectively, on the standard July-sown plot.

When the larval populations, for example those shown in fig. 4, are considered in relation to their respective egg populations, they all appear remarkably low, particularly the numbers of larvae which succeeded in reaching maturity. The total larvae of all ages on any sample occasion can be taken to represent the hatchings from the eggs laid over the previous three weeks. When these larval and egg populations are compared the mortality appears never to be less than 80 per cent., and at the end of the oviposition period in November and December it may rise to 100 per cent.

The exact cause of this high mortality is not immediately apparent. Larval parasitism was always extremely low, and consisted entirely of Dipterous parasites which emerged from the fully grown larvae after these had formed cocoons in the soil, and then formed their own puparia within the cocoon. The figures quoted in Table II are typical. Examples of one such parasite submitted to the Commonwealth Institute of Entomology is thought possibly to be *Carcelia illota* (Curr.) (Tachinidae). No egg-parasites were ever encountered, although many thousands of eggs were collected and allowed to hatch in tubes. Percentage hatching always ranged from 90–100 per cent., and the egg mortality observed could probably be ascribed to the effects of removing the egg from the plant during collection. There remain therefore predators and climate as possible causes of the high mortality. It is probable that both are involved, the former predominating throughout the season, and the latter becoming operative during the severe dry-season conditions in November and December. Thus, while the egg-counts give an indication of the period of moth activity and its relative intensity in different areas, the actual attack as measured by the larval counts may show quite a different picture.

Records from Kontagora and Gusau have shown the same seasonal pattern of oviposition on the cotton crop, the main difference being apparent at Kontagora, where egg-laying activity may continue until late January.

The occurrence of diapause.

Collection of full-grown larvae was started in October 1948, and continued at weekly intervals until December. These were collected from peasant farms in the Samaru area, and at each collection an estimate was obtained of the numbers of full-grown larvae present per acre. The larvae were placed in open-ended cages of perforated zinc, 4 in. square × 7 in. high, sunk into soil in concrete troughs containing 10 in. of sterilised soil (Pl. XLIII), and provided with green bolls to complete feeding and development. The internal dimensions

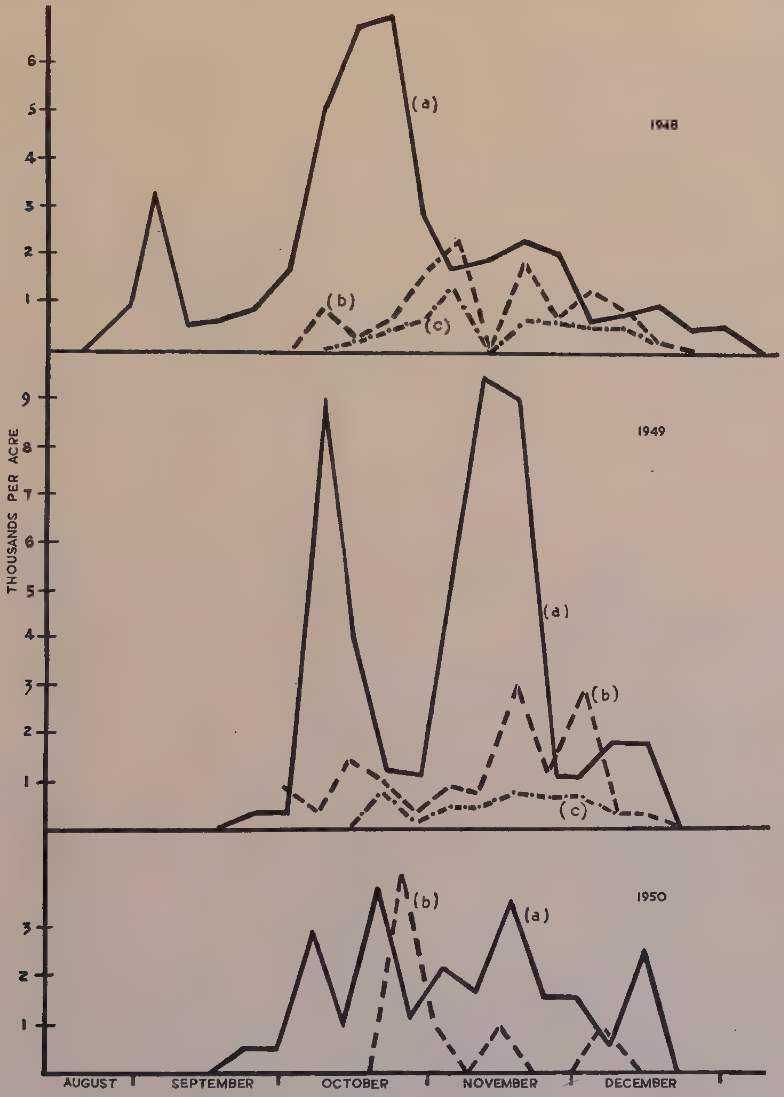


Fig. 4.—Populations of red bollworm, Samaru 1948–1950: (a) eggs laid per week; (b) total larvae; (c) full-grown larvae.

of the concrete troughs were 2 ft. 6 in. × 5 ft. × 1 ft. 6 in., and they accommodated 45 cages, each taking 10 larvae. They were provided with a water-channel to prevent the entry of predatory ants, and with drainage holes, towards which the floor of the trough had a slope of 1 in 60. This is a modification of the method employed in S. Africa for studies of *Heliothis armigera* (Hb.) and *D. castanea* (Parsons & Ullyett, 1934). When fully grown, the larvae entered the soil in the cages, formed earthen cells and pupated. The cages were provided with cloth covers, and examined daily for emerging moths. Soil thermometers recorded the soil temperature at 1½ in. in the troughs and in cotton fields, and shade over the troughs was adjusted to keep their temperatures as near as possible to those of the field. The temperatures recorded in these two locations are shown in fig. 3. After cotton is uprooted the soil above pupae in the fields is without shade, and the soil temperatures during March–June represent those under a bare fallow. Sorghum is normally planted after cotton, so that the moths emerging from diapause pupae usually come from under sorghum crops. The field temperatures from June to November were therefore recorded in a crop of sorghum.

The moths which emerged in 1948 from larvae matured in that year's cotton crop did so mainly in November, the larvae having been collected in October, while the remainder emerged at the end of December, from larvae collected in November. No moths were produced in 1948 from larvae collected in December. The cages were then left undisturbed until late May 1949 when the contents were carefully sieved, and the living diapause pupae detected by gently shaking the cells, of which those containing living pupae produce a distinctive rattle. The cells were then replaced in the cages in loose soil, and subsequent emergence noted. After this examination, it was possible to determine what proportion of the pupae from each week's collection in 1948 had remained in diapause. This is shown in Table I, where calculations are based only on living material.

TABLE I.

Red bollworm at Samaru, northern Nigeria, 1948. Development of diapause, and associated temperatures.

Period of collection of larvae	Average air temperatures		Average range °C.	Pupae in diapause (%)
	Max. °C.	Min. °C.		
19–25.ix	31	20	11	0
26.ix–2.x	31	20	11	0
3–9.x	32	21	11	0
10–16.x	33	18	15	5·5
17–23.x	33	17	16	9·7
24–30.x	33	16	17	37·8
31.x–6.xi	34	17	17	65·5
7–13.xi	32	18	14	78·5
14–20.xi	31	17	14	100·0
21–27.xi	30	14	16	100·0

This Table illustrates the sudden increase in development of diapause from the end of October. The climatic conditions associated with the period when diapause was induced can be seen from an examination of Table I and figs. 2 & 6. They were characterised by a steady and very rapid drop in relative humidity, and increasing diurnal range of temperature. Pearson & Mitchell found in Nyasaland that the formation of diapause pupae was associated with larval development under conditions where the minimum (boll) temperature was below, and the diurnal range exceeded, 20°C. No boll temperatures were obtained at Samaru, those in Table I referring to air temperatures. Larvae collected as fully-grown during any one week would have been subjected to the temperatures of the previous 2–3 weeks. The period when maximum diapause was induced thus appears to have been from 17th October onwards, when the maximum temperatures were highest, and the temperature range greatest. The latter was considerably less than 20°C., but the temperature of bolls would have shown a greater range. In general, however, *D. watersi* appears to behave similarly to *D. castanea* in this respect.

Emergence from diapause pupae.

In 1949, emergence from the pupation cages recommenced on 2nd June, only two days after the first eggs had been recorded in the field on cotton left standing from the previous season. (This is regarded as an indication that conditions in the cages were not markedly different from those in the field.) The subsequent pattern of emergence is shown in fig. 5. There were two periods of emergence from diapause pupae; the first extended from early June to early July, with a peak in late June (fig. 5, a). There was then a complete cessation of emergence from these pupae until the beginning of October, when the second emergence period began and continued until the end of October, with a well-defined peak in the middle of the month (fig. 5, c). The earlier emerging moths came from pupae formed in November and December, while the October emergence was mainly from pupae formed in the previous October. These observations are similar to the findings of Pomeroy (1925) at Ibadan. There he found that diapause pupae formed in January remained dormant longer than those formed in February, namely 300 days as compared with 276, and he also noted larvae on standover cotton in June.

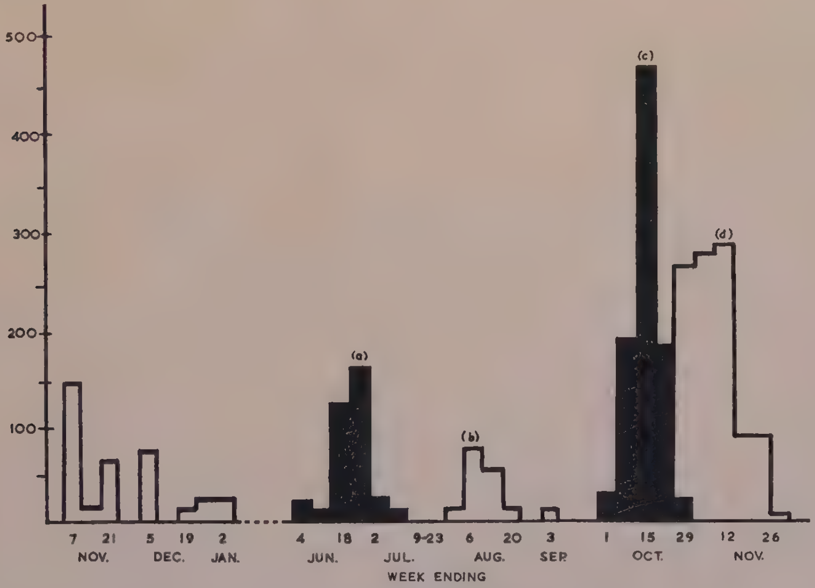


Fig. 5.—Number of red bollworm moths emerging per acre per week, Samaru, 1948–49.
Solid bars: Emergences from diapause pupae.
Open bars: Emergences from short-term pupae.

Short-term generations.

The first moths emerging in 1949 from diapause pupae oviposited during June and July on ratoon and standover cotton. Full-grown larvae collected from these and placed in cages produced entirely short-term pupae, from which moths emerged during late July and August (fig. 5, b). The moths emerging in October (from diapause pupae) attacked the main July-sown cotton crop, and gave rise to a generation of moths during November (fig. 5, d). In this month, however, 80 per cent. of full-grown larvae produced diapause pupae, and the attack showed a rapid decline, the last moths emerging in early December. If the graph of egg-laying for 1949 is consulted (fig. 4), it is apparent that the two peaks in October and November can be attributed to the moth emergences from diapause and short-term pupae respectively.

No details were obtained of the total length of the short-term life-cycle under the northern conditions. At Ibadan, however, Pomeroy gave the average length as 50 days (39 minimum, 64 maximum). Allowing a reduction for the higher temperatures encountered in the north, the range of development could be estimated as 30–50 days. Thus only those moths (bred in the crop) which emerged in late October or early November, and produced mature larvae before the end of November, could give rise to a second generation of moths, for no short-term pupae were formed after the end of November. It is probable that this is the usual state of affairs, *viz.*, that only one complete generation breeds in the main crop, and that the extent to which a partial second generation breeds would depend on the climatic conditions in November and early December. In both 1949 and 1950, there were no short-term pupae produced after the end of November.

Consideration of the bimodal emergence from diapause pupae.

The strongly bimodal emergence from resting pupae is a new feature in *Diparopsis* biology. A consideration of the climatic conditions during July to September, when the break in emergence occurs, suggests a possible explanation, *viz.*, frequent and heavy rainfall. The lower temperature limit for the slow development of diapause pupae of *D. castanea* in Nyasaland was 60°F. It is seen from fig. 3 that only once during this period did soil temperatures fall below this level. Temperature can therefore be ruled out as the factor preventing emergence, unless *D. watersi* differs greatly from *D. castanea* in this respect.

The emergence during August, however, of moths bred on ratoon cotton indicates that conditions were not inimical to short-term development. Under the rainfall conditions of July–September the Samaru soils become periodically waterlogged, and this may be the factor responsible for the break of emergence from diapause pupae. The effect of immersing pupae of *D. castanea* in water was studied in Nyasaland, and it was found that with diapause pupae, periodic immersion merely prolonged pupal life by the period of immersion; on the other hand, developing pupae, *i.e.*, short-term pupae, or diapause pupae which had recommenced active development, showed 0, 60 and 90 per cent. mortality after continuous immersion for 3, 5 and 7 days, respectively (Mitchell, 1942; Pearson & Mitchell, 1945*a*). The periods of waterlogging of the soil at Samaru were not determined exactly, but observation suggested they were of the order of 1–2 days in July, increasing to 3–5 in August and early September. In the cages there was a high mortality during late August and early September in the short-term pupae.

One can infer, therefore, that those diapause pupae which had not recommenced active development by early July were prevented from doing so by the soil conditions prevailing from then until early September; while the development of short-term pupae would be prolonged during July and early August, and they would then suffer a high mortality during late August and early September.

If the soil conditions were acting in this way to interrupt emergence, one could expect that emergence from pupae removed from the field but kept at comparable temperatures would show a different emergence pattern. This was tested in 1951. Diapause pupae were taken from cages on 25th May, divided into two batches, and incubated as shown under Table II.

The emergences up to the end of November are shown in Table II.

TABLE II.

Red-bollworm studies at Samaru, northern Nigeria, 1951. Fate of diapause pupae kept in laboratory. Figures expressed as percentages.

	Emergences								Unaccounted for	Pupae	
	Moths						Parasites	Total		Dead	Still alive
	June	July	Aug.	Sept.	Oct.	Nov.					
(a) Controlled	18·0	45·0	11·2	3·4	2·2	1·1	9·0	89·9	6·7	1·1	2·2
(b) Uncontrolled	2·2	12·4	47·2	14·6	2·2	0	7·9	86·5	10·1	1·1	2·2

(a) Under controlled conditions of 86°F. and 73 per cent. R.H.

(b) Under uncontrolled atmospheric conditions, *viz.*, 74–86°F. (mean 79·5°) and 65–84 per cent. R.H. (mean 76 per cent.).

These results clearly demonstrated that under both the controlled and the indoor atmospheric conditions, the emergence was unimodal, and it must be concluded that the physical conditions in the soil during July–September were responsible for the break in emergence which occurred in the field. Temperature can again be ruled out, as this follows closely—in excess of, air temperatures (fig. 6), which are shown above also to produce a unimodal emergence pattern.

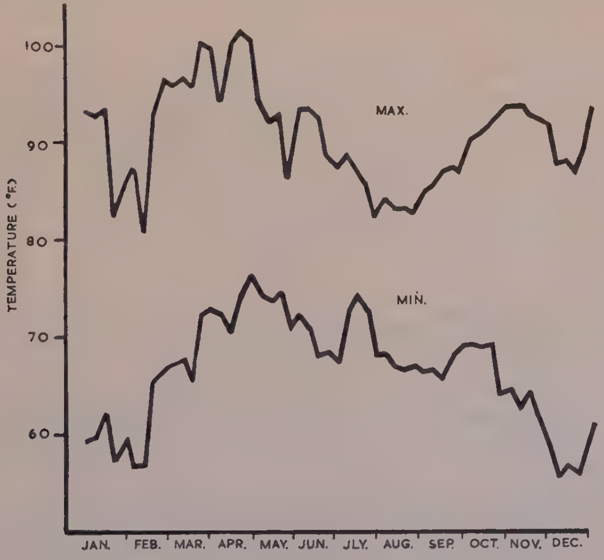


Fig. 6.—Weekly mean air temperatures, Samaru, 1949.

One returns therefore to a consideration of the effect of the heavy rainfall. This can affect the soil in two ways, both of which may result in poor aeration—*viz.*, waterlogging, when the air spaces in the soil are filled with water, and the formation of a surface seal, which also restricts aeration of the soil in which the pupae are buried. Both soil conditions would have the same effect as the immersion of pupae in water, *viz.*, deprivation of air. If this can be proved to be the operative factor, it immediately points to a possible method of controlling *Diparopsis* in this region, *i.e.*, by facilitating percolation of water, and thus improving aeration of the soil.

If the emergence from incubated pupae is a reliable indication of what it would be under these conditions, then the bulk of moths would emerge from diapause pupae during June–September, and the main crop would only receive the tail-end of the emergence in October. Before such a control measure could be attempted, however, it would be necessary to examine the physical conditions of the soil and subsoil, to see in fact whether the percolation and aeration of the soil could be improved, for example by the application of a mulch (Russell, 1950).

Bollworm activity in relation to the timing of the crop.

Under the present climatic and cultural conditions, the pattern of red-bollworm activity appears to be the same throughout the northern cotton belt—*i.e.*, an early emergence of moths from diapause pupae from late May to late July, followed by a break until October. The early emerging moths are able to produce one generation on ratoon and standover cotton left growing amongst the succeeding crops. A survey of the incidence of such cotton and associated red-bollworm populations was made in the Daudawa area in July 1949. Ratoon plants ranged from 120 to 1,800 per acre out of an original population of 14,000 per acre, and they occurred in all fields examined. On these, red-bollworm eggs ranged up to 5,000 per acre. In 1949 and 1950, plots of ratoon and standover cotton were observed at Samaru. In 1949, 50 per cent. of plants left standing had survived the dry season, and recommenced flowering in June. Oviposition by *Diparopsis* continued throughout June and July, with peak populations comparable with those found on peasant farms during July. It is apparent from these observations, and the emergence records, that the presence of ratoon and standover cotton may enable an early attack to develop in late August on an early-sown crop (*e.g.*, fig. 4, 1948). The elimination of ratoon and standover cotton would prevent this. This account, however, is based only on the observations of 1948–51, and only in the last three seasons was the complete cycle of activity determined. One must expect annual variations in the early and late emergences from diapause pupae, probably determined by climatic variations. In the absence of ratoons, the first emergence should be of no importance; and the importance of the second will depend on the time of its occurrence, and its intensity. The latter will be to some extent determined by the size of the first emergence.

Trials of Dates of Sowing.

In the light of the information given in the preceding sections, trials were laid down at Samaru and Daudawa in 1950, to see whether the effect of the main, second emergence of moths could be influenced by varying the sowing date. The period during which it is practicable for peasants to commence sowing is limited by the primary demand of food-crops, and the earliest possible time for sowing is in mid-June. Accordingly the following four dates were selected:

17th June: Early.
3rd July: Normal—earliest officially recommended date.
18th July: Normal—latest officially recommended date.
29th July: Late.

The layout of the plots in each locality was identical, *viz.*, six replicated blocks of the four dates of sowing. Throughout the season, in both localities, counts were made of red-bollworm eggs and larvae; the shedding of buds and bolls, and its causes, was also examined. Those bolls maturing were graded for bollworm and stainer damage and in addition, at Samaru only, on ten sample plants per plot, flowers were labelled as they opened. Their subsequent fate was then recorded, and in this way it was possible to ascertain over which periods the crop was formed on the different sowings, and when losses due to insects were incurred.

In considering the results of these trials, however, it is not possible to confine one's attention to *Diparopsis*. For, when examining yield differences, it is obvious that all other insects, notably other bollworms, and stainers, are involved. As far as possible the remarks will be confined to *Diparopsis*, because in both localities it was the dominant species, but for an adequate interpretation of the results, some mention will have to be made of the other insects.

When taking green-boll samples to record larval populations of *Diparopsis*, the numbers of larvae of *Argyroploce leucotreta* Meyr., *Platyedra gossypiella* Saund. and *Earias* spp. were also noted, but when grading the ripe crop, it is not possible to decide with certainty how much of the damage to ascribe to individual species. Such damage in the ripe crop was therefore generally ascribed to " bollworm ".

The red-bollworm attacks on the different sowings at the two localities, expressed as total eggs per acre laid during the season, are summarised in Table III.

TABLE III.

Red bollworm at Samaru and Daudawa, northern Nigeria. Date-of-sowing trials, 1950. Eggs laid per acre during whole season.

Sowing dates	Period of egg-laying	Days duration of oviposition	Total eggs per acre
Samaru			
A, 17th June	11.viii–24.xi	105	20,256
B, 3rd July	1.ix – 8.xii	98	15,085
C, 18th July	6.x –15.xii	70	8,375
D, 29th July	13.x – 8.xii	56	7,650
Standard sample plot (sown early July)	22.ix –15.xii	84	22,515
Daudawa			
A, 17th June	18.viii–19.i	154	187,115
B, 3rd July	15.ix –19.i	126	136,528
C, 18th July	29.ix –19.i	112	121,205
D, 29th July	13.x –19.i	98	161,100
Standard sample plot (sown early July)	25.viii– 5.i	125	102,000

Included for comparison are the figures from the standard plots that are laid down each year to obtain a picture of the attack in each locality. The total eggs laid was nearly five times as great at Daudawa as at Samaru. Moreover, although the start of egg-laying on each sowing differed by not more than two weeks from that on the corresponding sowing in the other area, the time of the attacks was such that at Samaru the percentage of total eggs laid before 1st October was, for the four sowings A–D, 48, 29, 0 and 0 per cent., respectively, while the corresponding figures for Daudawa were 1·8, 1·9, 0·5 and 0 per cent.

This illustrates the generally later commencement of attack at Daudawa, where oviposition continued much later than at Samaru, and there is a suggestion that breeding on the earlier sowings may have produced an exceptionally heavy attack on the latest sowing (D).

An analysis of the plot records showed that, at Samaru, the oviposition on sowings A & B were significantly greater than on C & D, although neither A and B nor C and D differed between themselves. At Daudawa, B and C showed a lower level of oviposition than the earliest and latest sowings, in which this was of the same order. It has already been mentioned that the egg-counts, while giving an accurate indication of the timing of an attack, are not a reliable measure of its intensity, due to a very high mortality in the young larvae. The larval counts obtained in the experiments were, however, unsatisfactory. This was partly because they did not cover the period when maximum numbers would be expected (as judged by egg-counts) on the earlier sowings, but chiefly because the size of the boll samples which it was possible to examine was inadequate to follow the population fluctuations at low levels. However, the samples taken were of the same size for each locality, and the total larvae recorded over each experiment can be taken to give some picture of the relative weight of attack in the two areas. On this basis, from the start of recording on 25th October, to 13th December, larval populations were 65 times greater at Daudawa than at Samaru.

The damage inflicted by bollworm is of two kinds. Firstly, young larvae feed mainly on flower buds or young bolls, and cause these to shed; the plant makes up this loss by the production of new fruiting points which must necessarily produce a later crop. If growing conditions are favourable for long enough, the plants can make good the whole loss, but the later in the season this sort of damage occurs, the less chance the plant has of maturing replaced bolls, and in this way loss of crop increases.

Secondly, older larvae feed on larger bolls, which if more than 10 days old will not shed, and the resulting loss of crop is seen in the eaten-out locules of ripe bolls. The damage can be directly determined, and when estimating losses due to bollworm damage on these trials, both types of damage had to be considered.

The loss resulting from shedding is very much the more difficult to determine. This is due to the cotton plant's habit of shedding young bolls and buds when climatic conditions become unfavourable for growth. It has been estimated in

TABLE IV.

Red bollworm in northern Nigeria, 1950. Date-of-sowing trials. Bolls shed per 60 plants during whole season.

	Sowing dates A 17 June	 B 3 July	 C 18 July	 D 29 July
Samaru				
Total bolls shed	845	505	554	610
Number undamaged by bollworm	754	453	497	594
Number damaged by bollworm	91	52	57	16
Percentage damaged by bollworm	10·8	10·3	10·3	2·6
Daudawa				
Total bolls shed	1,215	875	596	760
Number undamaged by bollworm	728	500	329	477
Number damaged by bollworm	487	375	267	283
Percentage damaged by bollworm	40·1	42·9	44·8	37·2

TABLE V.

Red bollworm in northern Nigeria, 1950. Date-of-sowing trial, Daudawa. Numbers of bolls shed per 60 plants.

Week ending	Sowing dates											
	A 17th June			B 3rd July			C 18th July			D 29th July		
	Non-BW.	BW.	% BW.	Non-BW.	BW.	% BW.	Non-BW.	BW.	%BW.	Non-BW.	BW.	% BW.
21st October	43	50	53·8	31	41	56·9	12	16	57·1	1	3	75·0
28th October	43	62	59·0	31	51	62·2	18	46	71·9	6	22	78·6
4th November	35	53	60·2	25	39	60·9	23	44	65·7	23	39	62·9
Totals	121	165	57·6	87	131	60·0	53	106	66·7	30	64	68·1
Total shedding	286			218			159			94		

other regions (and confirmed here) that, in the absence of any heavy insect attack, the plant sheds 75 per cent. of the bolls formed throughout the season. Thus, unless a very high proportion of these are damaged by bollworm, one cannot say whether bollworms alone are causing any loss by shedding. The situation, as regards boll-shedding, on these trials is well illustrated in Tables IV and V.

The very different levels of shedding in the two areas, and the low proportion due to bollworm at Samaru are illustrated in Table V; even at Daudawa, however, the proportion damaged by bollworm did not exceed 50 per cent. The season's total figure is misleading, because it includes the heavy "physiological shedding" which occurs at the end of the season in November and December. The shedding which is really important is that which occurs towards the end of the growing period, when those bolls are falling that could mature, but cannot be replaced by later-formed bolls.

This critical period appears to be during late October and early November. At Samaru, only during one week of this period were 50 per cent. of the shed bolls showing damage by bollworm, so that one must conclude that there, bollworm was having no influence on the crop in this way. The situation at Daudawa, as one might expect, was different and the proportion of the shed bolls that showed bollworm damage, during the period 14th October–4th November, is given in Table V.

Both before and after the above period the proportion of shed bolls damaged by bollworms on all sowings was less than 50 per cent., and in fact the heaviest total shedding occurred later in November, when the crop was losing all young bolls due to the onset of the severe dry-season conditions. The Table illustrates, however, the heavier total shedding on the earlier sowings, while the highest proportion damaged by bollworm was in fact recorded on the two later sowings. The heavier shedding on earlier sowings could be the result of the plants carrying more fruiting points as a result of their longer growing period. Clearly these sowings thus suffer less from bollworm than the later sowings which, with fewer fruiting points, anyway, lose a higher proportion to bollworm. It was only on these two latest sowings that bollworm appeared to be causing any loss of crop by shedding, over this period.

Examination of the ripe crop involves harvesting each boll separately, and recording the condition of individual locks. In this way damage due to bollworm and other insects, mainly stainers, can be determined. The results for these trials are shown in Table VI, where "stained" locks are those partially damaged by stainers, "rotten" locks are those completely lost as a result of severe stainer

TABLE VI.

Red-bollworm studies in northern Nigeria, 1950. Date-of-sowing trials. Analysis of damage to ripe crop (percentages of total harvested locks).

Sowing date	Clean		Bollworm		Stained		Rotten	
	Samaru	Daudawa	Samaru	Daudawa	Samaru	Daudawa	Samaru	Daudawa
A, 17th June	67·3	65·4	13·6	15·0	13·5	11·5	4·8	8·1
B, 3rd July	79·4	67·2	4·1	14·0	9·9	10·1	2·4	8·7
C, 18th July	90·6	75·3	2·7	14·2	5·5	5·3	1·3	5·2
D, 29th July	90·0	71·3	2·5	14·6	7·0	7·7	0·4	6·4

damage, or secondary bacterial rotting following bollworm attack, and "bollworm" locks are all those partly or completely destroyed by bollworm.

The two features to note here are (a) the higher proportion of clean cotton on the later sowings at Samaru, associated with less bollworm and stainer damage than the earlier sowings, and (b) the absence of any such differences at Daudawa. These can now be considered in conjunction with yields, Table VII.

TABLE VII.

Red-bollworm studies in northern Nigeria, 1950.
Date-of-sowing trials. Yields as lb. per acre
of Grade I seed cotton.

Sowing date	Samaru	Daudawa
A, 17th June ..	537	439
B, 3rd July ..	505	462
C, 18th July ..	481	336
D, 29th July ..	371	279

Considering Samaru first, the earliest sowings showed the lowest proportion of clean locks, and the highest proportion of bollworm damage; they yet gave the highest yields. The two latest sowings showed the converse of this. Such a result was obtained in an area where insect attack, mainly red bollworm and stainers, commenced and finished early. The effect of sowing early appears to have more than offset any increased insect attack. At Daudawa, the first two sowings again outyielded the two later sowings. Here, however, there were only slight differences between sowings in the proportions of bollworm or stainer damage to the ripe cotton. The increased yield on the earlier sowings could be ascribed partly to their earliness, and partly to their suffering less shedding due to bollworm, noted above. The general yield level was higher at Samaru than at Daudawa, but in both localities the advantage to be gained by early sowing is emphasised by the differences in yields.

The essential information obtained from the daily labelling of flowers at Samaru is illustrated as a histogram in fig. 7, where the total production of flowers in each week is shown, and their subsequent fate (as bolls) indicated by different shadings. This again illustrates the very small proportion of both shed and ripe bolls which were damaged by bollworm, and shows that the light attack came mostly on to the earliest sowing, in September and October. These observations provided, therefore, information only on the timing of a light, early bollworm attack on the different sowings. They showed clearly, however, that the greater part of all flowers produced after the end of October were subsequently shed as young bolls, and that the more flowers produced before then, the greater was the resulting crop. This late shedding of undamaged fruiting points can almost certainly be attributed to the severe dry-season conditions which, setting in at that time, acted as a guillotine to further crop production.

The very heavy boll shedding (not ascribable to bollworm) which occurred throughout September on the earliest sowing, was not associated with the same adverse climatic conditions; the exact cause was not apparent.

The main conclusion to draw from these trials is that, even in the absence of heavy red-bollworm attack, sowing in late June or early July produces higher yields by setting the crop before adverse environmental conditions set in at the end of October. If, on to this unalterable basic pattern, early bollworm attack is superimposed—as occurred at Samaru—the early sowing is already growing under optimum conditions, and producing a greater crop than a later sowing, more than sufficient to compensate for that lost to bollworm. It seems likely, that with a rigidly enforced close-season and elimination of ratoons, such an early sowing would perform even better than on this occasion, where the early

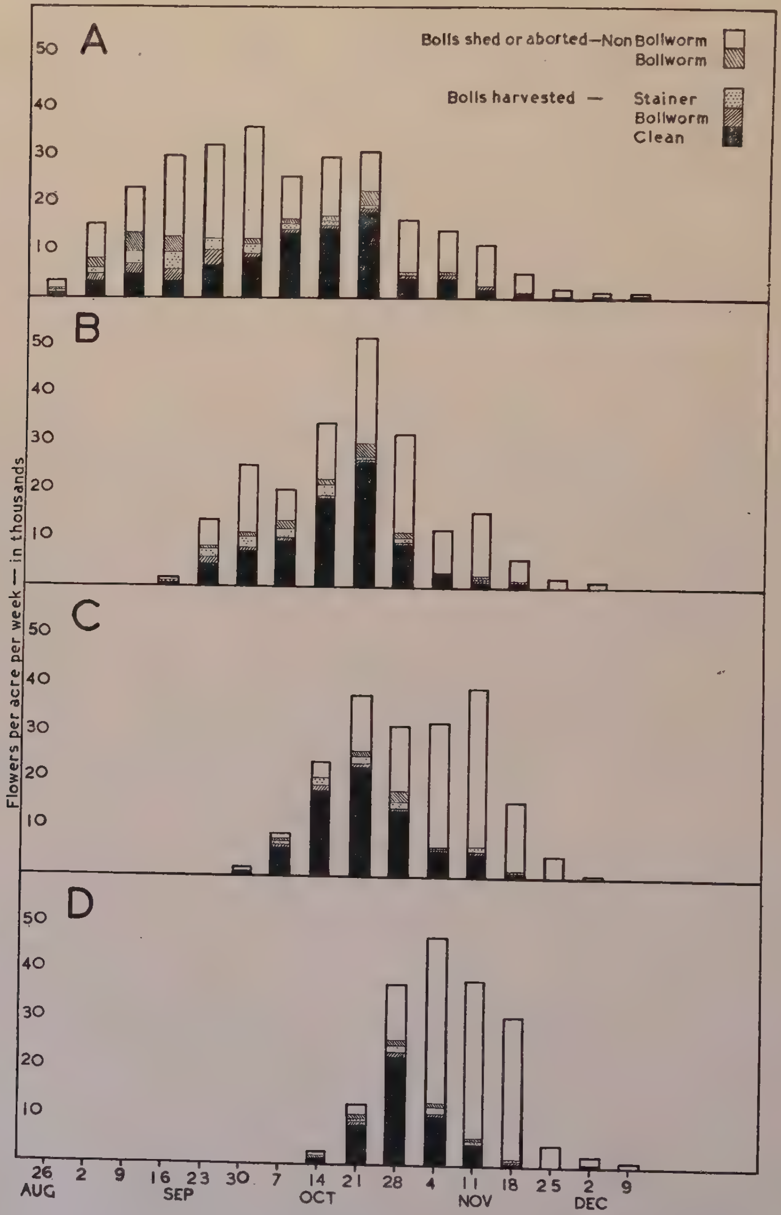


Fig. 7.—Production and fate of flowers, date-of-sowing trials, Samaru, 1950.

red-bollworm attack appeared to come from ratoon cotton. If, on the other hand, a later bollworm attack develops on the scale that occurred at Daudawa, no practicable alteration of sowing date will avoid it; but early sowing will produce a crop in the best possible condition to cope with such an attack.

Conclusions.

Control of an insect pest by evasion, *i.e.*, adjustment of sowing date, is frequently limited by the length of the growing season. In this instance, external environmental factors compel the cotton crop to grow and *Diparopsis* to breed within the same limited period, which makes such evasion difficult. The cotton crop cannot be sown by peasant farmers until food crops are assured, and the growing period is cut off by the onset of the dry season irrespective of sowing date. The main period of breeding of *Diparopsis* is delayed until October by the break in its emergence occasioned by the soil conditions in July–September, a factor which actually works in favour of the insect by ensuring its emergence when the crop is suitable for breeding. Subsequently its period of breeding is also limited by the dry-season conditions inducing diapause.

Under the present agricultural circumstances the best that can be done is, firstly, to eliminate ratoon and standover cotton, so that no early attack occurs, and secondly, to sow early, *viz.*, as near to mid-June as possible. This will ensure an optimum return of crop, not as a result of reducing the bollworm attack, but by making use of the longest possible growing season, in which the cotton plant more than makes good the greater loss due to bollworm. Later sowings, although they may suffer less damage, are unable to produce such a large crop by virtue of their short growing season. Clearly, if attempts are ever made to increase yields by the use of insecticides, it is the early sowings which will be more likely to repay the expenditure involved.

An alternative to insecticides, and probably a less expensive measure, would be to produce a unimodal emergence from the diapause pupae in the field. The factors involved in the bimodal emergence, and the possibility of altering these, would repay further study. If this alteration proved possible, it should result in control of the bollworm by evasion—in this case not by changing the sowing date, but by altering the time of the main emergence of the moths.

The distributions of the northern and southern species of *Diparopsis*, *i.e.*, *watersi* and *castanea*, are widely separated by the central equatorial zone of Africa (Pearson, 1949). The evidence available from the distribution in Africa of the wild indigenous species of *Gossypium*, and the other species of *Diparopsis*, suggests that the separation of the different species has been determined by the differentiation of the wild species of *Gossypium* (Hutchinson, 1954). *D. watersi* and *D. castanea* are, however, confined to similar ecological areas, and it is not to be expected that their biology would differ greatly; in fact, the main features appear to be identical. The only difference known is that whereas *D. castanea* breeds on *Cienfugosia hildebrandtii* in South Africa in addition to cotton (Marshall & others, 1937), no host other than *Gossypium* is known for *D. watersi*. Morphologically the two species are so similar that for many years the possibility that they were different was not contemplated. It would be of considerable interest to know to what extent crossbreeding between these two species is possible.

Summary.

The red bollworm attacking cotton in Nigeria has recently been shown to be *Diparopsis watersi* (Roths.), distinct from *D. castanea* Hmps., the southern African species previously assumed to be that occurring on cotton throughout Africa. Earlier work on cotton pests, including *Diparopsis*, in southern Nigeria is briefly reviewed, and the discovery and definition of the problems of cotton pests in northern Nigeria is outlined, and the climatic and agricultural background of the northern areas described.

The main object of the present work, centred at Samaru, was to determine the annual cycle of activity of *Diparopsis* in northern Nigeria. The methods employed are described. The insect passes the dry season in diapause as a pupa in the soil. In late May or June, emergence from these pupae commences, but this is completely interrupted during July–September. In October, after the end of the rains, emergence recommences, and the main attack occurs on the crop during October and November. The proportion of pupae entering diapause rises rapidly from mid-October onwards, and activity ceases in early December.

When diapause pupae were incubated at controlled (86°F.) or indoor air (74–86°F.) temperatures, emergence was unimodal, extending from June to October, with the peak in July or August, respectively. It is concluded that the bimodal emergence in the field is caused by waterlogging, or some other factor restricting aeration of the soil during July–September, when the emergence from diapause pupae is interrupted.

Trials of dates of sowing laid down at Samaru and Daudawa showed that early sowings, made in mid-June or early July, may suffer heavier bollworm attack than those made in mid- or late July. The earlier sowings nevertheless outyielded later ones. It is suggested that this results from their benefiting from a longer growing season, in which a greater production of fruiting points more than offsets greater losses from bollworms and other insects.

Elimination of ratoon and standover cotton would prevent breeding by the early emergence of moths from diapause pupae, and consequent red-bollworm attack on early sowings of cotton.

The possibility of producing a unimodal emergence from diapause pupae is worth further attention. This might be achieved by altering the soil conditions during July–September, and if successful would result in the main crop escaping almost entirely any attack by *Diparopsis*.

There appear to be no fundamental differences biologically between *Diparopsis castanea* and *D. watersi*, as illustrated by previous work reported from South Africa and Nyasaland, and the observations recorded here.

Acknowledgements.

The writers would like to thank the Director of Agriculture, Northern Region, Nigeria for permission to publish these results of work carried out while attached to his Department. Thanks are also due to Mr. E. O. Pearson, and Mr. M. A. Choyce, for reading and suggesting amendments to the draft.

References.

Baillie, A. F. H. & Geering, Q. A. (1952). Northern Nigeria . . . Entomology.—Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp. 1950–51, pp. 116–130.

Clements, A. N. (1951). A revision of *Diparopsis* Hmps. (Agrotidae, Lepidoptera).—Bull. ent. Res., **42**, pp. 491–497.

Geering, Q. A. (1950). Nigeria . . . Entomology.—Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp., 1948–49, pp. 126–136.

Geering, Q. A. (1951). Northern Nigeria . . . Entomology.—Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp., 1949–50, pp. 100–112.

Golding, F. D. (1928). A first survey of insect and fungoid incidence on improved Ishan cotton.—7th Annu. Bull. Dep. Agric. Nigeria, pp. 17–37.

Golding, F. D. (1929). Further surveys of insect and fungoid incidence on improved Ishan and other cottons in Nigeria.—8th Annu. Bull. Dep. Agric. Nigeria, pp. 110–129.

Golding, F. D. (1945). The occurrence of *Platyedra gossypiella*, Saund. in Nigeria.—Emp. Cott. Gr. Rev., **22**, pp. 1–2.

Golding, F. D., Lean, O. B. & Laycock, T. (1927). A critical comparison of the factors inhibiting the development of three species of cotton in Southern Nigeria.—6th Annu. Bull. Dep. Agric. Nigeria, pp. 5–69.

Hutchinson, J. B. (1954). New evidence on the origin of the Old World cottons.—Heredity, **8**, pp. 225–241.

Lean, O. B. (1927). Comparative observations on the pests of cotton at Ilorin, Northern Nigeria.—6th Annu. Bull. Dep. Agric. Nigeria, pp. 127–143.

Marshall, J., Parsons, F. S. & Hutchinson, H. (1937). Studies on the Red Bollworm of Cotton, *Diparopsis castanea*, Hampson. Pt. 1. The distribution and ecology of two natural food-plants, *Cienfuegosia hildebrandtii* Gürke, and *Gossypium herbaceum* var. *africana*, Watt.—Bull. ent. Res., **28**, pp. 621–632.

Mitchell, B. L. (1942). Nyasaland. Entomological work. Progress report. The Lake Shore area.—Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp., 1940–41, pp. 166–172.

Parsons, F. S. & Ullyett, G. C. (1934). Investigation on the control of American and Red Bollworms of Cotton in South Africa.—Bull. ent. Res., **25**, pp. 349–381.

Pearson, E. O. (1949). Problems of insect pests of cotton in tropical Africa.—Emp. Cott. Gr. Rev., **26**, pp. 85–99.

Pearson, E. O. (1954). The relationship between the African and South American Red Bollworms of Cotton, *Diparopsis* and *Sacadodes*.—Emp. Cott. Gr. Rev., **31**, pp. 171–177.

Pearson, E. O. & Mitchell, B. L. (1945*a*). Nyasaland. Entomological work.—Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp., 1943–44, pp. 145–153.

Pearson, E. O. & Mitchell, B. L. (1945*b*). A report on the status and control of insect pests of cotton in the Lower River districts of Nyasaland.—48 pp. Zomba, Nyasaland, Govt. Printer.

Pomeroy, A. W. J. (1925). The Cotton Bollworms of Southern Nigeria.—4th Annu. Bull. Dep. Agric. Nigeria, pp. 89–108.

Pomeroy, A. W. J. & Lean, O. B. (1925). Observations on the extent of the damage caused by Bollworms and Stainers to the cotton crop in Southern Nigeria.—4th Annu. Bull. Dep. Agric. Nigeria, pp. 50–63.

Russell, E. J. (1950). Soil conditions and plant growth.—8th edn., pp. 584–585. London, Longmans, Green.

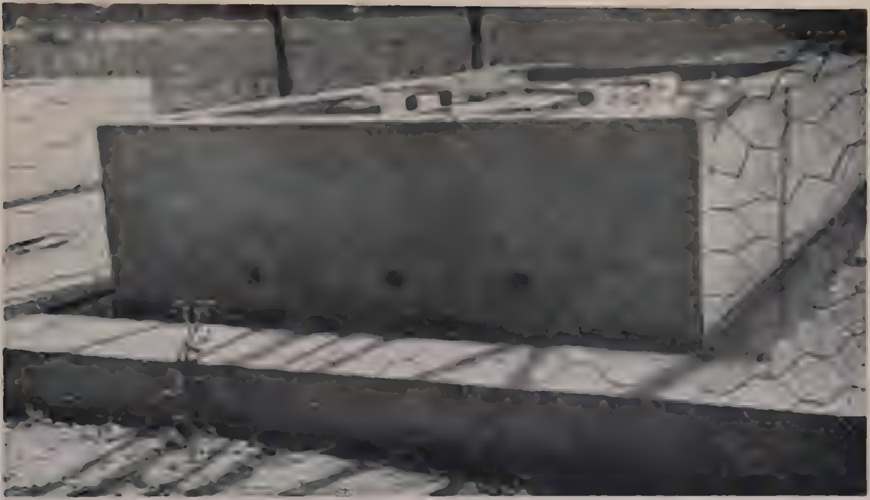


FIG. 1. Concrete pupation trough, illustrating the water-channel and drainage holes.

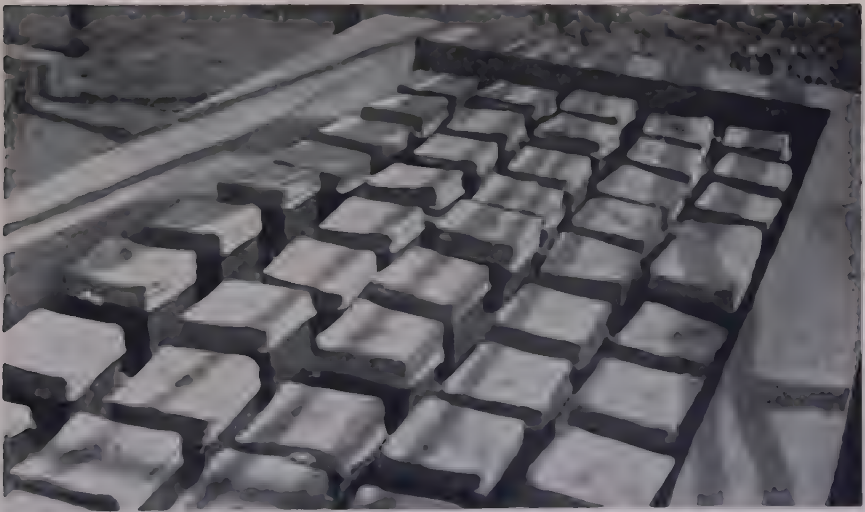


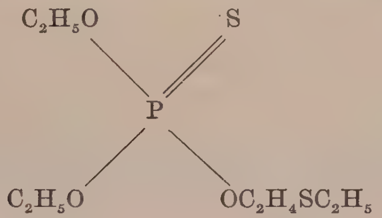
FIG. 2. Concrete pupation trough, illustrating arrangement of cages, and shade produced by sorghum stems.

THE ACTION OF THE SYSTEMIC INSECTICIDE SYSTOX, ON APHIDS.

By W. A. L. David and B. O. C. Gardiner.
Agricultural Research Council, Unit of Insect Physiology, Cambridge.

The work described in this paper has been carried out with two samples received from the Farbenfabriken Bayer Company of Leverkusen in 1951.

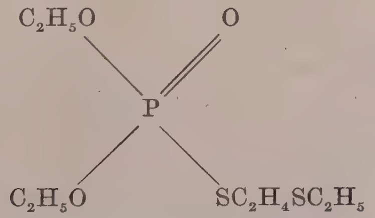
The first, Systox 50 emulsion, was stated to contain 50 per cent. of active ingredient and 50 per cent. emulsifier. Later, a sample of the active material designated E 1059 was obtained. It was said to have the structural formula



(S:POC)

O,O-diethyl O-ethylmercaptoethyl thiophosphate.

The same code number is used for this compound by Schrader (1952). It has subsequently been shown (Gardner & Heath, 1953) that the active ingredient in Systox 50 emulsion can be separated by chromatography into the compound shown above and the isomer



(O:PSC)

O,O-diethyl S-ethylmercaptoethyl thiophosphate.

The sample of Systox 50 emulsion which they examined contained 48 per cent. of active material, 18 per cent. being S:POC and 30 per cent. O:PSC, the active ingredient thus contained 37·5 per cent. S:POC and 62·5 per cent. O:PSC. The second example, referred to above as E 1059, consisting of the active material alone, has also been analysed and shown to contain 50 per cent. of the O:PSC compound (L. J. Bellamy, personal communication, 1953). The remainder was not analysed, but was assumed to be S:POC. Two other samples of Systox 50 emulsion have been examined by other workers who found that the active material contained 50 and 60 per cent., respectively, of the O:PSC compound (D. F. Heath, personal communication, 1953). The figures for the S:POC compound were not reported. The most recent information from the

Bayer Company (November 1953) gives the ratio P=S:P=O as 68:32, which is almost the reverse of that found in the older samples.

In this paper, the word " Systox " used on its own means the mixture of toxic isomers O:PSC and S:POC, whether from Systox 50 emulsion or as E 1059. The source, however, is indicated. For Systox 50 emulsion the specified 50 per cent. active material content is accepted.

Methods and Equipment.

The tests were carried out in a greenhouse in which the temperature generally fluctuated between 17–23°C. and the length of day was extended, where necessary, to 16 hrs. by fluorescent lighting. Ventilation was supplemented by extraction fans (David & Gardiner, 1951).

Three species of Aphids have been used in these tests:

The Bean Aphis, *Aphis fabae* Scop., reared according to the revised methods described by Kennedy & Booth (1954).

The cabbage Aphids, *Brevicoryne brassicae* (L.) and *Myzus persicae* (Sulz.), were reared in the production line used previously to produce *A. fabae* (Kennedy & Booth, 1950) or, when parasites were not troublesome, on cabbage plants in the greenhouse.

The bean plants, *Vicia faba*, were grown in " whalehide " pots of 3½-in. diameter, either in John Innes pasteurised potting compost or in sand watered once a week with nutrient solution. The cabbage plants were grown in the same way in compost.

The aphid population on the plants was not counted, instead it was assessed as follows:

Normal: Thriving colonies with Aphids of all stages settled and feeding, or a few adults surrounded by young.
Declining: Colonies with few Aphids, some dead Aphids on and around the plant, and the remaining Aphids often moving restlessly about.
Isolated: Only scattered individual Aphids and no young. Many dead Aphids around the plant.
Nil: No Aphids on the plant.

Besides the immediate toxic effect, the persistence of the material was also investigated. Attempts were made to reinfest treated plants 2, 5 and 10 days after the beginning of the experiment. The toxic condition shown by the plant at the time of the reinfestation was then described as:

High (H): All insects killed within 2 days of reinfestation.
Medium (M): All insects killed within 5 days of reinfestation.
Low (L): Some deaths, but an incomplete kill in 5 days.
Nil: No effect observed.

In making these assessments the following symbols were also used:

>: Indicates that the condition referred to was passed before an observation was made or between observations.
<: Indicates that the condition referred to was not reached in the course of the test.
O: Indicates that tests could not be made for the condition referred to.

(The signs >, <, and 0 have been used to replace the single sign (—) used in previous papers, in order to make it easier to interpret the results.)

Control groups or colonies of insects were kept in all experiments and where no reference is made to these, they remained normal.

Phytotoxicity was assessed as follows:

Normal (N):	Plant not different from control.
Trace (T):	Slight marginal scorch or wilt or scattered spotting.
Moderate (M):	Large areas of the leaves scorched or pronounced wilting.
High (H):	Plant almost entirely killed, though the small leaves around the growing point may still be green.
Dead (D):	Plant dead.

Potted plants may show various symptoms of ill health not attributable to treatment with the insecticides. In evaluating leaf damage the plants were therefore carefully compared with two or three untreated plants.

Experiments with *Aphis fabae* on Broad Beans.

Dipping tests.

The bean plants used in this experiment were specially prepared by cutting off the tops, leaving only the lowest pair of leaves. These were infested 24 hours before giving the treatment, which consisted of dipping the infested leaves into solutions of the insecticides. Systox 50 contains an emulsifier, but 0·1 per cent. Teepol was added to the E 1059 as a wetting agent and this strength of Teepol was used for treating the controls. Care was taken not to immerse the cut stem, and any Aphids on the undipped part of the plant were brushed off.

TABLE I.

Dipping tests with the two samples.

Material from	Systox (1) %(v/v)	Aphids First day on which			Toxic condition of plants			
					Last day			First day Nil
		Declining	Isolated	None	High	Med.	Low	
Systox 50 emulsion ..	0·05	>	>	1	2	10	15	<
	0·005	>	>	1	0	5	10	15
	0·0005	>	>	1	<	<	2	0
	0·0001	<	<	<	<	<	<	1
E 1059	0·005	>	>	1	<	<	<	2
	0·0005	>	1	<	<	<	<	2

Both samples were tested on 17.vii.52 and again on 2.ix.52.

(1) As always in this paper, Systox means the active ingredient.

From the result given in Table I it can be seen that the E 1059 solutions are slightly less toxic and definitely less persistent than the Systox 50 solutions. These differences could well be due to the different wetting agents present in the two solutions. This suggestion is rather confirmed by the fact that when applied systemically the two materials are equitoxic.

Systox is highly toxic to Aphids when applied in this way. By comparison with the result previously obtained (David & Gardiner, 1951), it appears to be about equitoxic with paraoxon (diethyl p-nitrophenyl phosphate) and so more toxic than schradan (octamethyl pyrophosphoramide) and dimefox (bis-(dimethylamino) fluorophosphine oxide).

Systemic action following applications made to the roots.

Plants growing in sand or soil.—The plants were grown to about 6 inches height in pots which held about 570 gm. of moist sand or 400 gm. of soil.

The doses of insecticides were made up to 20 cc. and poured on to the sand or soil. Subsequently 20 cc. of water were given to each plant daily. The watering had sometimes to be repeated on hot days. The aim was to keep the plants adequately watered while ensuring that there was no surplus water to drain from the pots.

The results obtained are given in Table II. It appears that there is very little difference between applying the active material as Systox 50 emulsion or as E 1059. As in the case with other systemics the insecticide is more effective in sand than in soil (David & Gardiner, 1951).

TABLE II.

Insecticide watered on to the sand or soil in which the plants were growing.

Material from	Systox applied (cc.)	Plants in	Aphids First day on which:			Toxic condition of plants Level/day
			Declining	Isolated	None	
Systox 50 emulsion ..	0·01	Sand	>	1	2	H/10
	0·002		1	>	2	H/10
	0·001		2	3	4	M/10
	0·0002		3	5	7	L/10
	0·0001		3	5	9	Nil/10
	0·00002		<	<	<	Nil/1
E 1059	0·001	Sand	2	4	6	M/10
	0·0002		3	5	7	Nil/10
	0·0001		3	4	<	Nil/10
	0·00002		<	<	<	Nil/1
Systox 50 emulsion ..	0·02	Soil	>	1	2	H/10
	0·01		1	>	2	H/10
	0·002		2	4	5	H/10
	0·001		3	5	6	M/10
	0·0002		<	<	<	Nil/1
E 1059	0·001	Soil	3	5	7	L/10
	0·0002		<	<	<	L/1

Dates of application of insecticide, 16.iv.52, 24.iii.52 and 25.iii.52.

Compared with the systemic insecticides previously tested, Systox is about equal to the most toxic, sodium fluoroacetate, and consequently more toxic systemically than paraoxon, schradan or dimefox.

There is a large safety margin between the dose required to free a plant of Aphids, 1 mg. per 400 gm. of soil, and that causing a trace of damage to the plant, which was 20 mg. per 400 gm. of soil. There is a similar large safety margin with plants growing in sand.

In a further experiment of the same kind, with the plants growing in soil, the insecticide was applied when the plants were about 2 inches high and observations were continued for 32 days until they were 3 ft. high. At the end of the test the treated plants were remarkably healthy while the control plants were smaller and stunted by a heavy population of Aphids. The results are given in Table III.

TABLE III.

A long-period experiment with the Systox added to soil in 20 cc. solution on 2.ix.53.

Systox applied (cc.)	Aphids First day on which: Declining	Isolated	None	Toxic conditions of plants Last day High	Medium	Low	First day Nil
0·01	1	>	3	25	<	<	<
0·001	5	6	9	10	>	15	25

In persistence also Systox compares favourably with the compounds previously tested. There was no evidence of phytotoxicity at the end of the experiment.

Plants in culture solutions.—The bean plants were grown in sand watered periodically with culture solution. They were used when 4–8 inches high, at which time they weighed 8–15 gm. The test solutions were contained in half-pint milk bottles plugged with cotton-wool. As the Aphids on the control plants standing among the test plants remained normal, it may be assumed that in this test the solutions did not exert a direct fumigant action. The plants were given 100 cc. of solution and this was renewed after 5 days. The results are shown in Table IV.

TABLE IV.

Plants in Systox solutions which were renewed every 5 days (March and April 1952).

Material from	Systox % v/v	Aphids First day on which: Declining	Isolated	None
Systox 50 emulsion	0·01	>	>	1
	0·005	>	>	1
	0·001	1	2	3
	0·0005	2	3	4
	0·0001	8	9	<
E 1059	0·005	>	>	1
	0·001	1	2	3
	0·0005	2	3	4
	0·0001	8	9	<

The solutions derived from Systox 50 emulsion and E 1059 were equitoxic in the test. Only the 0·01 per cent. solution from Systox 50 emulsion caused visible injuries to the plants and here the damage was classified as moderate.

Concentration of Systox in the plants necessary to kill the aphids.—It is possible to get a known dose of insecticide absorbed rapidly by bean plants by cutting the tap-root at a suitable point and placing it in a small tube containing about 1 cc. of the insecticide. When transpiration is rapid, absorption is complete in about 2–3 hours (David & Gardiner, 1951).

TABLE V.

Bean plants given 1 cc. each of the toxic solutions by the cut tap-roots.

Material used and date	Systox (%) v/v	Calculated conc. in plant (1) (mg./kg.)	Aphids First day on which:			Toxic condition of plants Level/day
			Declining	Isolated	None	
Systox 50 emulsion .. 13.viii.52	0·05	33	1	>	2	H/5
	0·01	7·0	1	2	4	M/5
	0·005	3·0	2	4	5	Nil/5
Systox 50 emulsion .. 16.ix.52	0·005	3·8	1	2	4	M/5, Nil/10
	0·001	1·0	3	7	10	Nil/10
	0·0005	0·4	<	<	<	Nil/1
E 1059 .. .. 4.xi.52	0·005	3·1	1	2	3	L/5
	0·001	0·6	5	<	<	L/1

(1) Milligrammes of Systox dosed per kg. of fresh plant tissue.

It may be seen from Table V that a dose equivalent to about 1 mg. of Systox per kg. of fresh bean tissue gives complete kills of *A. fabae* by the tenth day. A comparison with previous results (David & Gardiner, 1951) shows that at this concentration it apparently acts more slowly than sodium fluoroacetate, which gave complete kill in three days, though in the absence of a simultaneous comparison this is not definitely established. It should not be assumed that this quantity of the mixed isomers exists in the plant, as there is evidence that Systox breaks down very rapidly after absorption (G. S. Hartley, D. F. Heath, L. A. Lickerish, & P. O. Park, unpublished report, 1953).

Absorption by the intact roots.—Roots in the soil are often in a damaged condition and it seemed desirable to establish whether Systox could be absorbed through intact roots. The method used to obtain plants with undamaged roots was as follows. The beans were sprouted in sand in 5-in. clay pots. When the plants were about 2 in. high they were unpotted and the roots washed thoroughly. The lower part of the tap root was cut off and the bean was suspended in a covered beaker with the shoot outside and the roots just in water. After a few days, when fresh lateral roots had grown, the roots were again inspected and trimmed if necessary to remove any damaged roots. The water in the beaker was then replaced by the Systox solution to such a depth that only the tips of perfect roots were immersed. The top of the plant was screened from any possible direct vapour action by a ventilated lamp glass.

Under these conditions 0·001 per cent. solutions of Systox kill the aphid population entirely in two days—which is just as rapidly as when no care is taken to eliminate damaged roots.

Systemic Action following Application to the Leaves.

Several experiments were carried out in order to determine whether Systox was absorbed by the older leaves of bean plants and translocated in sufficient quantity to kill Aphids on the untreated younger parts of the plant. In these experiments the untreated part of the plant was screened from the treated leaves by a lamp glass ventilated by a slow stream of compressed air (David & Gardiner, 1953). The insecticide solutions were applied to the leaves with a camel-hair brush.

TABLE VI.

Effect on Aphids established on the younger leaves of broad beans of brushing the older leaves with Systox solutions.

Systox % v/v	No. of leaves		Treatments		Aphids First day on which:		
	Treated	Untreated	Total no. of applications	Days on which given (successive)	Declining	Isolated	None
0·10	4	Crown (1)	12	3	2	6	7
0·05	4	Crown	12	3	2	5	<
0·01	3	Crown	9	3	<	<	<
0·25	3	Crown	1	1	>	>	1
	5	Crown	1	1	>	1	3
	4	Crown	1	1	1	>	2
0·10	4	Crown	1	1	6	<	<

Tests carried out March, August and November 1952.

(1) The small unexpanded leaves of the growing point.

From Table VI it can be seen that, when applied to the older leaves, Systox is rapidly translocated to the younger untreated parts of the plant in sufficient quantities to kill Aphids. Occasionally the action is much slower.

The Fumigant Action of Systox.

Systox solutions exert a direct fumigant action on Aphids. Thus when a petri dish containing 1·0 or 0·1 per cent. v/v solutions of Systox is placed within 1–1½ inches of an aphid colony on a bean leaf all the insects are killed about one day later. The effect is naturally more intense in a closed system. A similar fumigant action of Systox on *Drosophila* has been reported by Lusis (1952).

The question whether plants treated systemically with Systox give off a toxic vapour will be discussed in a later paper.

Experiments with *Brevicoryne brassicae* and *Myzus persicae* on Cabbage Plants.

The methods and conditions adopted in these experiments were essentially the same as those used in the foregoing tests with *A. fabae*. Young cabbage plants about 6 in. high, growing in the usual 3½-in. diam. "whalehide" pots, were infested with the Aphids at least 24 hours before the insecticide was applied. Only Systox derived from Systox 50 emulsion was used in these tests.

TABLE VII.

Systox solutions (20 cc.) watered on to the soil in which cabbage plants were growing.

Insect	Systox applied (cc.)	Aphids			Toxic condition of plants			
		First day on which:			Last day			First day
		Declining	Isolated	None	High	Medium	Low	Nil
B. brassicae	0·020	>	>	1	20	<	<	<
	0·002	>	>	1	15	<	<	<
	0·001	>	>	1	5	10	15	<
	0·0002	>	>	1	<	5	>	10
	0·0001	>	1	2	<	<	5	10
M. persicae	0·002	>	>	1	10	>	20	<
	0·001	>	1	2	5	10	>	20
	0·0002	2	4	10	<	<	<	10
	0·0001	5	<	<	0	0	1	0

Tests carried out on 24.iii.52, 8.iv.53 and 9.v.53.

Systemic action following applications made to the roots.

Twenty cc. of the solutions containing the required amount of Systox were watered on to the soil in the "whalehide" pots in which the plants were growing (Table VII).

Both species of Aphids feeding on cabbages are killed by Systox at a lower dosage per pot than is necessary for *A. fabae* on broad beans. It has been shown by Day & Irzykiewicz (1953) that, when feeding on the Chinese cabbage (*Brassica chinensis*), *M. persicae* ingests twenty times as much plant material as *Brevicoryne brassicae*. If this ratio held in our experiments it might be expected that *Myzus* would be more readily killed than *Brevicoryne*, but in fact the reverse is true. The cabbage plants remained quite normal in appearance and there was no evidence of leaf scorch at the concentration used.

Systemic action following application to the leaves.

Evidence of translocation from the older, outer leaves of the cabbage plants to the untreated younger leaves was sought, taking the usual precautions to prevent material reaching the soil directly and to exclude direct fumigant action. After a single application the results obtained were very variable (Table VIII). This is a common experience in tests with systemic insecticides and there is an obvious need to investigate the factors which influence the quantity of insecticide translocated following applications made to the leaves, but clearly the untreated younger leaves may sometimes acquire a concentration toxic to the Aphids. That variations in the quantities translocated do occur is confirmed by some experiments with radioactive Systox which will be the subject of a later report. The treated leaves were often scorched, sometimes seriously, by the Systox solutions and there is some evidence that high levels of leaf damage were correlated with high concentrations of translocated insecticide.

Summary and Conclusions.

The work described in this paper has been carried out with two proprietary samples, designated Systox 50 emulsion and E 1059, of a systemic insecticide of which the active ingredient, subsequently referred to throughout as Systox, is a mixture of O,O-diethyl O-ethylmercaptoethyl thiophosphate and its isomer, O,O-diethyl S-ethylmercaptoethyl thiophosphate.

The samples were tested against Aphids for contact and systemic action.

It is concluded that, as a contact insecticide against *Aphis fabae* Scop. on broad beans, Systox is about equitoxic with paraoxon and so more toxic than schradan and dimefox.

TABLE VIII.

Effect on Aphids established on the unexpanded leaves of the crown of cabbage plants of brushing the older leaves with Systox solutions.

Insect and date of treatment	Systox % v/v	No. of leaves treated (¹)	Aphids First day on which: Declining	Isolated	None	Level of damage to treated leaves on 2nd day
B. brassicae						
5.vi.53 ..	1·0	3	>	>	1	M
		3	2	<	<	M
25.vi.53 ..		3	>	1	2	H
		3	>	1	2	H
5.vi.53 ..	0·5	3	2	3	<	M
		3	>	>	1	M
25.vi.53 ..		3	>	1	<	T
		3	>	1	<	T
14.v.53	0·25	4	<	<	<	N
			<	<	<	N
M. persicae						
5.vi.53 ..	1·0	3	<	<	<	T
		3	<	<	<	T
25.vi.53 ..		3	>	>	1	H
		3	3	4	1	H
5.vi.53 ..	0·5	3	2	4	5	N
		3	<	<	<	N
25.vi.53 ..		3	<	<	<	N
		3	>	>	1	N

(¹) In each experiment one small leaf and the unexpanded leaves of the crown were left untreated.

Systox is readily absorbed by the roots of broad bean and cabbage plants from soil, sand and aqueous solutions and the translocated material is very effective as an insecticide against *A. fabae* on broad bean, and *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.) on cabbage.

Applied in this way, Systox is more effective than schradan, dimefox and paraoxon, and about equal to the most toxic compound previously tested, sodium fluoroacetate.

An experiment by the cut tap-root technique confirms these conclusions. A dose of 1 mg. of Systox per kg. of fresh bean-plant tissue gave a complete kill of *A. fabae* by the 10th day. The same amount of sodium fluoroacetate had previously been shown to give a complete kill in three days.

The plants were carefully watched for signs of damage during the tests. It was concluded that there was a considerable margin between the insecticidally effective and the phytotoxic concentrations.

Systox is also translocated from older to younger leaves of bean and cabbage plants and it may reach concentrations sufficient to kill the Aphids feeding on the untreated leaves. This effect was more consistently obtained in the broad bean than in cabbage plants. In both cases, however, the results were variable.

Solutions of Systox exert a direct fumigant action on Aphids, but there is little evidence that toxic material is transpired by treated plants.

Acknowledgement.

We would like to thank Dr. L. J. Bellamy, Ministry of Supply Chemical Inspectorate, for analysing the sample of active ingredient.

References.

David, W. A. L. & Gardiner, B. O. C. (1951). Investigations on the systemic insecticidal action of sodium fluoroacetate and of three phosphorus compounds on *Aphis fabae* Scop.—Ann. appl. Biol., **38**, pp. 91–110.

David, W. A. L. & Gardiner, B. O. C. (1953). The systemic insecticidal action of sodium fluoroacetate and of three phophorus compounds on the eggs and larvae of *Pieris brassicae* L.—Ann. appl. Biol., **40**, pp. 403–417.

Day, M. F. & Irzykiewicz, H. (1953). Feeding behaviour of the Aphids *Myzus persicae* and *Brevicoryne brassicae*, studied with radiophosphorus.—Aust. J. biol. Sci., **6**, pp. 98–108.

Gardner, K. & Heath, D. F. (1953). Quantitative determination of isomers of O,O-diethyl ethylmercaptoethyl thiophosphate.—Analyt. Chem., **25**, pp. 1849–1853.

Kennedy, J. S. & Booth, C. O. (1950). Methods for mass rearing and investigating the host relations of *Aphis fabae* Scop.—Ann. appl. Biol., **37**, pp. 451–470.

Kennedy, J. S. & Booth, C. O. (1954). Host alternation in *Aphis fabae* Scop. II. Changes in the Aphids.—Ann. appl. Biol., **41**, pp. 88–106.

Lusis, E. (1952). The effect of " Systox " on *Drosophila melanogaster* Mg.—Höfchenbr. Wiss. (Engl. edn.), **5**, pp. 225–238.

Schrader, G. (1952). Die Entwicklung neuer Insektizide auf Grundlage organischer Fluor- und Phosphor-Verbindungen.—Monogr. angew. Chem. & Chem.-Ing.-Tech., no. 62, 2nd edn., 96 pp. Weinheim, Verlag-Chemie.

THE ACTION OF THE SYSTEMIC INSECTICIDE SYSTOX, ON *PIERIS BRASSICAE* (L.) AND *PHAEDON COCHLEARIAE* (F.).

By W. A. L. David and B. O. C. Gardiner.

E.H.N.

Agricultural Research Council, Unit of Insect Physiology, Cambridge.

The generally favourable reports on the systemic insecticidal action of Systox against Aphids and the observation that it gave outstanding protection of the young plant when applied to certain seeds before sowing made it seem desirable to test it against other pests. The results obtained with *Aphis fabae* Scop., *Brevicoryne brassicae* (L.) and *Myzus persicae* (Sulz.) have already been reported (David & Gardiner, 1954*b*) and a report on the seed-soaking investigation is in preparation. The present paper discusses the effect of Systox on the eggs and larvae of *Pieris brassicae* (L.) and on the eggs, larvae and adults of *Phaedon cochleariae* (F.).

In this paper, as in the one mentioned above dealing with Aphids, the word " Systox " is used to mean the mixture of toxic isomers which occurs in Systox 50 emulsion (50 per cent.) and other preparations. The figures in the Tables and elsewhere thus all refer to the quantity of actual toxic mixture present calculated on the stated composition. Systox is a mixture of two isomeric compounds, O,O-diethyl O-ethylmercaptoethyl thiophosphate and O,O-diethyl S-ethylmercaptoethyl thiophosphate. For further discussion of its composition reference should be made to Gardner & Heath (1953) or more briefly David & Gardiner (1954*b*).

Methods and Equipment.

The insects and plants were kept and the experiments were conducted in the greenhouse previously described (David & Gardiner, 1952).

The *Pieris* were obtained from a laboratory culture maintained all the year round (David & Gardiner, 1952). To encourage mating, the adult cage should be at 27°–30°C. while the lamp that gives a sunlight effect is on. At other times it can be cooler (20°C.). Plenty of rough surfaces, such as muslin, to provide easy footholds for the adults are also necessary in this cage. During the tests the larvae were confined on cabbage plants in wire-gauze cages (David & Gardiner, 1953).

The *Phaedon* were reared, and handled during the test as previously described. They were confined on turnip test-plants in glass-ring cages (David & Gardiner, 1954*a*).

For both insects the percentages killed in the tests were recorded daily. All the tests were run in duplicate and repeated. In certain cases the average temperatures in the greenhouse during the confirmatory test was subsequently found to be appreciably different from those occurring during the original test. In such cases both sets of figures are reported since they are more instructive than average values. The deaths among the controls were very few in most cases and they were neglected. Figures for the controls are therefore usually only reported when this was not the case.

Tests with Eggs and Newly-hatched Larvae.

Contact action.

The leaves of young plants bearing eggs were dipped individually into solutions of Systox, kept at 18°–20°C. and a systemic effect *via* the roots was guarded against (David & Gardiner, 1953). At the time the eggs were dipped, the *Pieris* eggs were 2–3 days old and the *Phaedon* eggs 2 days old. The results are given in Table I. The *Pieris* eggs developed but the larvae were killed about the time at which they first punctured the shells. The tests with *Phaedon* eggs were unsatisfactory (David & Gardiner, 1954*a*), but at least it may be seen that the concentrations used did not kill all the eggs or prevent the emergence of the larvae. When the larvae emerged they were not killed by feeding on the dipped leaves.

TABLE I.

Cabbage and turnip leaves bearing eggs dipped into Systox solutions.

Systox % v/v	Percentage of eggs not hatching	
	Pieris	*Phaedon*
0·1	100	<25
0·01	90	<25
0·001	0	—
Control	0	<25

Dipped 19.vii.52 and 3.ix.52.

Systemic action following absorption by the root from soil.

The young cabbage plants bearing *Pieris* eggs were treated by watering 20 cc. of the insecticidal solutions containing the required amount of insecticide on to the compost in the 3½-in. diam. " whalehide " pots, containing about 400 gm. compost, in which they were growing. The *Pieris* eggs were 1–2 days old when the plants were watered and they began to hatch eight days after treatment. The results are given in Table II. In tests with *Phaedon*, owing to a series of

TABLE II.

Systox solution watered on to soil in which cabbage plants were growing.

Systox present in 20 cc. solution (cc.)	*Pieris*	
	%of eggs not hatching	% kill of larvae
0·16	100	—
0·08	100	—
0·04	75	100
0·02	50	70

poor hatches among the eggs on the control plants, no satisfactory results were obtained. No toxic effects were noticed on the cabbage plants.

It is evident that Systox, like diethyl p-nitrophenyl phosphate (paraoxon) may be absorbed by the roots of cabbage plants and prevent the emergence of the larvae from the shells, though a dosage of about 0·08 cc. per 400 gm. of soil is required, compared with 0·01 cc. or less, previously found for paraoxon (David & Gardiner, 1953).

Systemic action against Pieris *on cabbage plants following absorption by the leaves.*

Penetration through the leaves.—Unless a systemic insecticide applied to one surface of a leaf can prevent the hatching of eggs on the other surface, opposite to the point of application, it is unlikely that a toxic effect will be shown when translocation for greater distances within the plant are involved. In the first tests the ability of Systox to pass through the leaf was therefore tested. The insecticide solutions were brushed on to the upper surface of the leaf exactly over the eggs on the under surface. The arrangement adopted to exclude direct fumigant action around the margin of the leaf is shown in fig. 1. The eggs (A) are laid on the leaf (B) which rests on the perspex plate (C) in which a round hole has been cut. On top of the leaf is a sponge-rubber washer (D) on which a cylinder (E) rests and this is weighed down by a nut (F). The insecticide is applied to the leaf surface within the cylinder. At the time of the application the eggs were two days old. It can be seen from Table III that Systox solutions are capable of penetrating young cabbage leaves and preventing the hatching of *Pieris* eggs on the undersurface. The results obtained are rather variable except at the highest concentrations. Only about 1 sq. in. of the leaf surface was treated and it was observed that eggs in batches not exactly

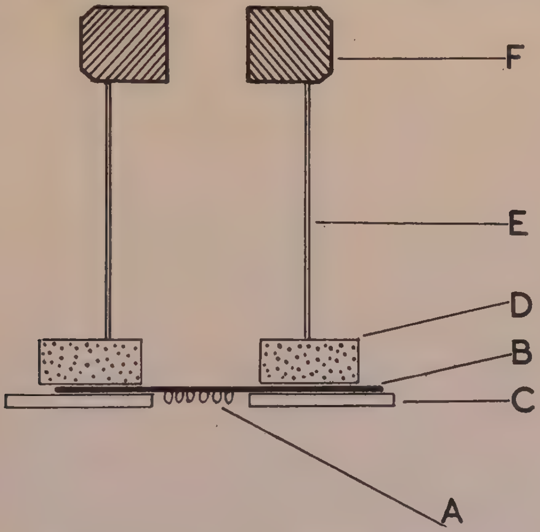


Fig. 1.—Diagrammatic transverse section of the arrangement adopted to investigate the effect of Systox solutions applied to the upper surface of the leaf on *Pieris* eggs on the undersurface. (A) eggs; (B) leaf; (C) perspex plate; (D) sponge-rubber washer; (E) cylinder; (F) weighting nut.

under the point of application of the insecticide were also sometimes killed. With the 0·5 per cent. solutions, marginal leaf-scorch distal to the area treated was observed.

Applied in this way Systox is much less effective than paraoxon, for while 0·5 per cent. solutions of Systox were required to give a certain 100 per cent. prevention of hatching of eggs, the same effect was obtained with 0·001 per cent. solutions of paraoxon (David & Gardiner, 1953). The figures in the Table for percentage kill of larvae were obtained before the larvae had eaten through to the treated surface of the leaf.

Translocation from older to younger leaves.—No effect could be obtained with 0·1 per cent. Systox solutions. All the eggs on the young untreated leaves

TABLE III.

Systemic action of Systox solutions, brushed on to the upper surface of a cabbage leaf, on the eggs and larvae of *Pieris* on the undersurface (October to December 1952).

Systox % v/v	Plant no.	Percentage of eggs not hatching	Percentage kill of larvae by 2nd day after hatching
0·50	1	100	—
	2	100	—
0·20	3	100	—
	4	100	—
	5	90	100
0·10	6	90	0
	7	95	100
	8	25	100
	9	100	—
0·01	10	100	—
	11	75	100
	12	0	0
	13	0	0

TABLE IV.

Third-instar *Pieris* and second-instar *Phaedon* larvae dipped in Systox solutions.

Systox % v/v	*Pieris* Percentage of larvae dead by day		*Phaedon* Percentage of larvae dead by day	
	2	5	2	5
0·40	70	70	—	—
0·20	10	20	60	70
0·10	0	0	42	47
0·05	—	—	15	18
0·01	—	—	0	0

Dates: *Pieris* 31.vii.52 and 2.ix.52; *Phaedon* 28.vii.52, 30.x.52 and 4.ii.53.

hatched normally and the larvae were normal. The same result was obtained with paraoxon (David & Gardiner, 1953).

Tests with Second- and Third-Instar Larvae.

Contact action.

The larvae were covered with the solutions at 20°C. for half a minute, transferred to dry filter-paper and then to the leaf of the food plant. There was a good deal of variability in the results and the figures in Table IV are the averages of four or six batches. It can be seen, however, that Systox solutions are very much less effective than paraoxon solutions. The latter give 100 per cent. kills of *Pieris* and *Phaedon* larvae at about 0·01 per cent. (David & Gardiner, 1953, 1954*a*).

Feeding on dipped foliage.

In these tests five or ten larvae were allowed to feed on the leaves of young plants which had been dipped in Systox solutions and then dried. The results obtained in two tests are summarised in Table V. The temperature in the greenhouse was lower in the second test on each insect (see Table V, footnote) and the kills were also lower. As in the case of direct-contact tests, *Phaedon* larvae are more susceptible to Systox than *Pieris* larvae. Systox is again less toxic than paraoxon, which killed *Pieris* larvae at 0·01 per cent. and *Phaedon* larvae at 0·005 per cent.

TABLE V.

Second- and third-instar *Pieris* and second-instar *Phaedon* feeding on leaves of cabbages and turnips, respectively, dipped in Systox solutions.

Systox % v/v	*Pieris*				*Phaedon*			
	Date	%of larvae dead by day:		% of treated foliage eaten by 4th day	Date	% of larvae dead by day:		% of treated foliage eaten by 4th day
		2	5			2	5	
0·20	(1) 31.vii.52	60	100	<5	(3) 29.ix.52	100	—	<5
	(2) 18.ix.52	0	80	25–50	(4) 7.x.52	60	100	<5
0·10	31.vii.52	30	70	<5	29.ix.52	55	100	<5
	18.ix.52	0	50	25–50	7.x.52	5	100	<5
0·01	31.vii.52	0	0	90	29.ix.52	5	75	50
	18.ix.52	0	0	100	7.x.52	0	35	75
0·001	—	—	—	—	29.ix.52	0	0	90
					7.x.52	0	0	90
Control	All	0	0	100	All	0	0	90

Temperatures (°C.) over test period: (1) av. 20·4, max. 26, min. 16; (2) av. 18·7, max. 26, min. 11; (3) av. 19·6, max. 24, min. 17; (4) av. 18·2, max. 24, min. 14.

Systemic action following absorption by the roots from soil.

The method for treating the plant has already been described in the section on eggs and young larvae. The required dose was watered on to the soil five days before the *Pieris* larvae were allowed to begin feeding on the cabbage plants and four days before the *Phaedon* were allowed to feed on the turnip plants. The results are given in Table VI.

In this test, as in the others, *Phaedon* larvae were more susceptible than *Pieris* larvae to Systox. *Pieris* larvae are less susceptible to Systox than to paraoxon, which gave the same results at about one-fiftieth of the dose. The results in the case of *Phaedon* are not directly comparable.

TABLE VI.

Systox solutions watered on to soil in which plants are growing.

Systox present in 20 cc. solution (cc.)	*Pieris* % of larvae dead by day: 2	*Pieris* % of larvae dead by day: 5	*Pieris* % of foliage eaten by 5th day	*Phaedon* % of larvae dead by day: 2	*Phaedon* % of larvae dead by day: 5	*Phaedon* % of foliage eaten by 5th day
0·10	70	100	<5	—	—	—
0·02	0	40	<5	90	100	<5
0·01	0	10	90	70	100	<5
0·002	0	0	90	15	100	50
0·001	—	—	—	0	75	90
Control	0	0	>90	0	0	>90

Dates: *Pieris* 25.vii.52; *Phaedon* 29.ix.52.

Systemic action following absorption by the leaves.

Systox at concentrations up to 0·5 per cent. active ingredient were brushed on to the older, outer leaves of cabbage and turnip plants for several days. The 0·5 per cent. solution scorched the treated leaves and neither this nor the lower concentrations produced any detectable effect on the larvae, which consumed the young untreated leaves and grew normally.

Tests with *Phaedon* Adults.

Tests were conducted with *Phaedon* adults following the procedures that have been described for the larvae earlier in this paper and by David & Gardiner

TABLE VII.

Adult *Phaedon* exposed to Systox by dipping or by allowing the beetles to feed on dipped turnip foliage.

Systox %	Dipping % of adults dead by day: 2	Dipping % of adults dead by day: 5	Feeding on dipped foliage % of adults dead by day: 2	Feeding on dipped foliage % of adults dead by day: 5
0·20	100	—	100	—
0·10	85	95	40	95
0·05	80	85	—	—
0·01	15	20	0	40
0·001	0	0	0	0

Date: 20.x.52.

(1954*a*). The results of the contact tests and the tests in which adults were allowed to feed on dipped foliage are given in Table VII. Two tests in which the plants were treated by watering the insecticide on to the soil are reported in Table VIII; these systemic tests show that a higher average greenhouse temperature is associated, as would be expected, with a higher kill of beetles.

When the Systox is applied systemically the adults require a higher dosage than do the larvae to suffer a complete kill.

TABLE VIII.

Systox solutions watered on to soil in which turnip plants carrying adult *Phaedon* are growing.

Systox present in 20 cc. solution (cc.)		Percentage adults dead on day:		% of leaf eaten by day:
		2	5	5
0·02	(a)	20	100	<5
	(b)	30	95	<5
0·01	(a)	0	35	<5
	(b)	35	80	<5
0·002	(a)	0	15	—
	(b)	10	55	50
0·001	(a)	0	5	—
	(b)	0	20	175 (¹)
Control	(a)	—	—	—
	(b)	0	0	200 (¹)

(a) Date 16.viii.52, temperature (°C.), av. 18·1, max. 24, min. 15.

(b) Date 24.x.52, temperature (°C.), av. 20·3, max. 25, min. 17.

(¹) These figures indicate that a second leaf was provided for the larvae.

The Systemic Toxicity of Systox to *Pieris* Larvae.

Known volumes of Systox solutions of various concentrations were fed to the cut leaves of cabbage plants from small specimen tubes as previously described (David & Gardiner, 1953). When the solutions were all absorbed the larvae were allowed to feed on the leaves under petri dishes ventilated with saturated air. After 24 hours the larvae and the remainder of each leaf were weighed. The results are given in Table IX.

In the case of leaves exposed to larvae the loss of weight which occurs during the 24-hour test period cannot be apportioned between evaporation loss and the feeding of the larvae. The loss of weight of the control leaf due to evaporation was about 12 per cent. and losses above this amount indicate that larvae have been feeding. A gain in weight by the larvae during the test period indicates that the leaf tissue is not sufficiently toxic to prevent growth, while a loss of weight beyond the 8 per cent. lost by starving larvae indicates a definite toxic action. Looked at in this way, Table IX indicates that Systox fed to a cut cabbage leaf caused it to become sufficiently toxic to prevent growth of *Pieris* larvae at between 140 and 310 mg. per kg. of fresh leaf tissue. These values are about 30 to 80 times those found for paraoxon by the same method (David & Gardiner, 1953) and are in line with the conclusions drawn earlier in this paper (p. 698) that 50 times as much Systox as paraoxon had to be watered on to the soil in order to produce the same effect.

The Fumigant Action of Systox Solutions.

It has previously been reported that Systox solutions have a strong fumigant action and will kill *Drosophila* (Lusis, 1952) and Aphids (David & Gardiner, 1954*b*) exposed to them. By enclosing *Pieris* larvae in a glass ring on a muslin platform over 1·0 per cent. Systox solutions it was shown that all the larvae were affected on the second day, moribund on the third and dead on the fourth day. A 0·1 per cent. solution produced an equally rapid action. *Phaedon* adults were all killed in two days when exposed in a similar manner to 1·0 per cent. solutions. When the insects were caged in a glass ring with a muslin floor which was about 0·5 cm. above a leaf dipped in 0·2 per cent. Systox solution and dried they were not affected.

TABLE IX.

The dosages of Systox fed to cut cabbage leaves and the effect of the treated leaves on *Pieris* larvae.

Concentration of solution fed to leaves (% v/v)	Conc. of material in leaves (mg./kg.)*	Average weight of larvae used (gm.)	Weight lost by leaf (%)	Weight lost or gained by larvae (%)
0·5	1415	0·205	9·2	−50·6
0·1	311	0·177	13·9	−50·7
0·05	141	0·186	31·2	+58·6
Water	0	0·156	48·0	+176
Water	0	No larva	12·4	—
No leaf	—	0·153	—	−7·9

* Calculated on fresh leaf tissue.

Discussion.

The experiments are on the whole quite straightforward and their interpretation presents no problems which have not been dealt with in earlier papers. Investigations of the properties of the two isomers contained in Systox and of the absorption of the more toxic of the two by plants have been carried out and will be reported in a later paper.

It remains to consider whether Systox could be usefully employed to control *Pieris* or *Phaedon*.

In the case of *Pieris* eggs, a complete prevention of larval emergence was obtained by wetting them with an 0·1 per cent. solution, but between 0·2 and 0·5 per cent. solutions must be applied to the upper surface of the leaves to kill eggs on the under surface and the latter concentration is liable to cause leaf scorch. Still, in the tests only a small area of the leaf was treated and with a complete cover spray a satisfactory control by translocation through the leaf might be obtained at lower concentrations. Translocation from treated to untreated leaves did not occur in sufficient quantity to give a control. When applied to the soil a rather large dosage is required to prevent the eggs hatching. The experiments with *Phaedon* eggs were unsatisfactory but suggested that Systox was unlikely to give a practical control.

Against the larvae, Systox is not an outstanding contact insecticide, more than 0·4 per cent. v/v being required to give complete kills or *Pieris*, while 0·2 per cent. does not give a complete kill of *Phaedon*. When fed on dipped foliage, *Pieris* larvae are all killed when a 0·2 per cent. solution has been used and *Phaedon* after a 0·1 per cent. solution. When applied to the soil, so that it acts systemically, about 100 times as much is required to kill *Pieris* larvae as was required to kill Aphids. *Phaedon* larvae on the other hand are killed by about the same dose as Aphids (0·002 cc. per 3½-in. diam. pot). By feeding the solutions directly to the leaves it has been estimated that the dose required to kill all the Aphids on a plant in one day is between 7 and 33 mg./kg. of fresh leaf tissue, whereas somewhere between 140 and 310 mg./kg. are required to stop the growth of *Pieris* larvae within one day. Systemic action against the larvae feeding on the younger leaves, following applications to the older leaves, could not be obtained at concentrations up to 0·5 per cent., which caused leaf scorch.

Some of the more important of these conclusions are summarised in Table X.

TABLE X.

Comparison of the approximate amounts of Systox and paraoxon required to give complete kills of *Aphis fabae*, *Pieris* larvae and *Phaedon* larvae and adults.

Material	Method of dosing						
	By dipping in a solution: % concentration giving complete kill			Systemically *via* the soil: cc. per pot (1) giving complete kill			
	A. fabae	*Pieris*	*Phaedon* adults	*A. fabae*	*Pieris*	*Phaedon* larvae	*Phaedon* adults
Systox ..	0·0005	>0·4	>0·2	0·001	0·1	0·002	0·02
Paraoxon ..	0·0005	0·01	0·01	>0·04	0·002	0·001	0·002

(1) 3½-in. diameter pots containing about 400 gm. compost.

Obviously, Systox is much less effective against *Pieris* and *Phaedon* than against Aphids, except as a systemic insecticide applied to the roots against *Phaedon* larvae on turnips. If the need arose, Systox might be worth considering for this purpose and also for controlling the hatch of *Pieris* eggs.

Summary.

The mixture of O,O-diethyl O-ethylmercaptoethyl thiophosphate and O,O-diethyl S-ethylmercaptoethyl thiophosphate, known as Systox, which has been previously tested against Aphids, has now been tested as a systemic insecticide against the eggs and larvae of *Pieris brassicae* (L.) and the eggs, larvae and adults of *Phaedon cochleariae* (F.).

Systox is toxic by direct contact to all stages of these insects but is much less effective in this way than diethyl p-nitrophenyl phosphate (paraoxon).

As a systemic insecticide applied to the roots of the host-plant, Systox again acts on all stages of the insects (except the eggs of *Phaedon*), but, compared with the dose which killed Aphids, about twice as much is required to kill

Phaedon larvae and between 20 and 100 times as much to kill *Pieris* larvae, depending on the method employed.

When applied systemically Systox, like paraoxon, can prevent the emergence of *Pieris* larvae from the eggs.

References.

David, W. A. L. & Gardiner, B. O. C. (1952). Laboratory breeding of *Pieris brassicae* L. and *Apanteles glomeratus* L.—Proc. R. ent. Soc. Lond., (A) **27,** pp. 54–56.

David, W. A. L. & Gardiner, B. O. C. (1953). The systemic insecticidal action of sodium fluoroacetate and of three phosphorus compounds on the eggs and larvae of *Pieris brassicae* L.—Ann. appl. Biol., **40,** pp. 403–417.

David, W. A. L. & Gardiner, B. O. C. (1954*a*). The systemic insecticidal action of certain compounds of fluorine and of phosphorus on *Phaedon cochleariae* Fab.—Ann. appl. Biol., **41,** pp. 261–270.

David, W. A. L. & Gardiner, B. O. C. (1954*b*). The action of the systemic insecticide, Systox on Aphids.—Bull. ent. Res., **45,** pp. 683–692.

Gardner, K. & Heath, D. F. (1953). Quantitative determination of isomers of O,O-diethyl ethylmercaptoethyl thiophosphate.—Analyt. Chem., **25,** pp. 1849–1853.

Lusis, E. (1952). The effect of " Systox " on *Drosophila melanogaster* Mg.—Höfchenbr. Wiss. (Engl. edn.), **5,** pp. 225–238.

TWO NEW SPECIES OF MIRIDAE (HEMIPTERA-HETEROPTERA).

By N. C. E. Miller, F.R.E.S., F.Z.S., F.E.S.S.A.
Commonwealth Institute of Entomology, London.

Specimens of the first of the new species here described were received by the Commonwealth Institute of Entomology from Mr. G. Swaine, Entomologist to the Department of Agriculture, Tanganyika Territory, who reported it as injurious to shoots and young fruits of the cashew nut, *Anacardium occidentale* L., and of the second through the British Museum (Natural History) from Mr. G. S. Dun, Senior Entomologist, Division of Plant Industry, New Guinea.

Helopeltis anacardii, sp.n. (fig. 1).

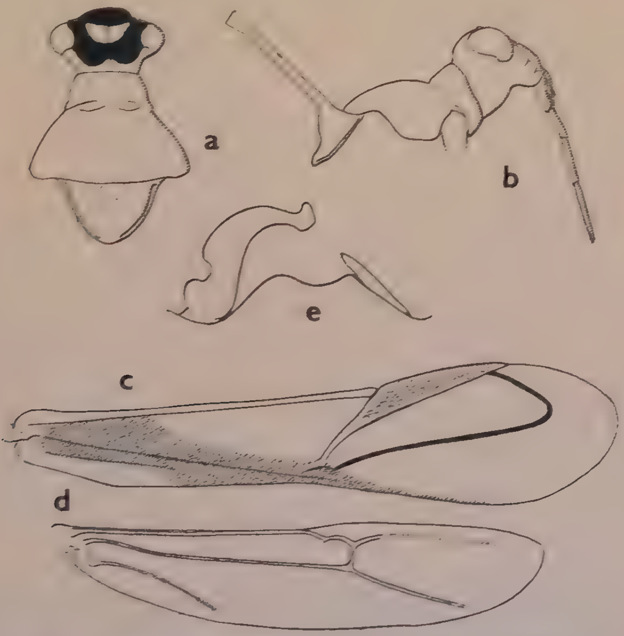


Fig. 1.—*Helopeltis anacardii*, sp.n. *a*, head, pronotum and scutellum, dorsal view; *b*, *idem*, lateral view; *c*, hemelytron; *d*, metathoracic wing; *e*, apex of pygophore, terminal view.

Colour: Basal segment of antennae stramineous, narrowly suffused with piceous apically; segments 2 and 3 blackish; segment 4 missing. Head, body, legs, except tarsi, yellow; tarsi piceous. Head with a piceous spot between antennae and a transverse piceous stripe on postocular coalescing with it. Pronotum and abdomen dorsally suffused with light red. Scutellum whitish; spine yellow. Hemelytra hyaline, faintly yellow; corium basally and along anal margin faintly infumate; clavus very faintly infumate; cuneus suffused with red; venation of membrane fuscous. Abdomen ventrally yellowish white.

Structure: Size small. Basal segment of antennae, 3·30 mm.; segment 2, 5·00 mm.; segment 3, 4·00 mm.; segment 4 missing in all specimens examined. Rostrum extending to or a little beyond median coxae. Pronotum smooth; posterior lobe obscurely rugose; calli moderately prominent. Scutellar spine moderately slender, feebly curved backwards; apex truncate (This is due to the collapse of the less sclerotised part.)

	♂	♀
Total length	4·50 mm.	6·00 mm.
Hemelytra	5·00 mm.	6·00 mm.
Greatest pronotal width ...	1·40 mm.	1·70 mm.

10 ♂♂ (one of which the type), 3 ♀♀, Tanganyika Territory, Lindi. 4.x.1953 (*G. Swaine, Department of Agriculture*). On *Anacardium occidentale* L. (ANACARDIACEAE). The type is deposited in the British Museum (Natural History).

Developmental stages: Third- and fifth-instar larvae yellowish white dorsally; ventrally white. Antennae, head, pronotum, rudimentary hemelytra, connexival segments and apex of scutellar spine suffused with light red; femora with apex and obscure annulations light red; tibiae suffused with light red. Abdomen dorsally with an irregular, transverse light red stripe. Total length: 3rd instar, 3·00 mm.; 5th instar, 4·00 mm.

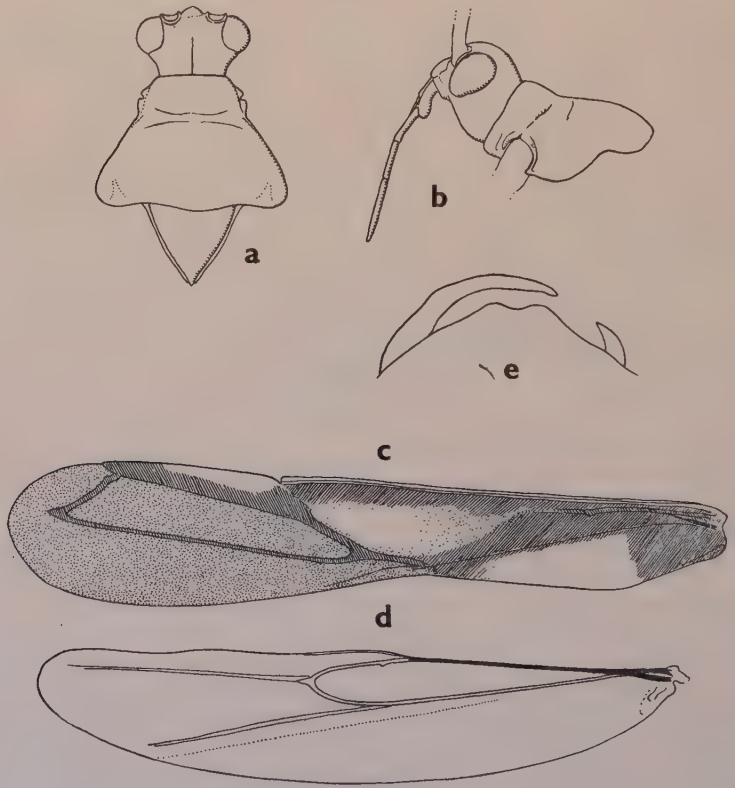


Fig. 2.—*Eucerocoris festivus*, sp.n. *a*, head, pronotum and scutellum, dorsal view; *b*, *idem*, lateral view; *c*, hemelytron; *d*, metathoracic wing; *e*, apex of pygophore, terminal view.

Helopeltis anacardii, sp.n., differs from all known species in colouration and is much smaller than known Ethiopian species. It differs from *Helopeltis schoutedeni* Reuter (1906, Ent. Mag. Lond., **42,** p. 112) in the relatively wider vertex (between antennae), less strong constriction between anterior and posterior pronotal lobes, in the regularly rounded gular region (in profile), thicker scutellar spine, the apex of which is larger, the venation of the membrane and in the genitalia.

Eucerocoris festivus, sp.n. (fig. 2).

Colour: Antennae piceous; basal segment suffused with red. Rostrum, gular region, sterna, pleura and abdomen pale yellow. Head dorsally piceous; vertex laterally suffused with red and with a median, elongate yellow spot. Pronotum and scutellum piceous, the former suffused with dark yellow medially. Legs stramineous, except tarsi, dark brown. Corium pale yellow with the following areas dark vinaceous,—base, apex and internal margin of clavus, costal and apical areas (except external margin of costa), internal margin and apex of cuneus; apex of clavus and pale area of corium with infumate suffusion. Membrane infumate with vein of cell vinaceous.

Structure: Basal segment of antennae thickened in apical fourth, 2·50 mm.; segment 2, 4·00 mm.; segment 3, 2·50 mm.; segment 4, 1·00 mm.; segments 2–4 with short, forwardly directed setae. Head and body glabrous. Rostrum extending to middle of mesosternum. Hemelytra extending beyond apex of abdomen by a little less than half their length. Femora moderately incrassate apically; tibiae and tarsi with abundant, short, forwardly directed setae.

	♂	♀
Total length	4–4·50 mm.	5·60 mm.
Hemelytra	6·00 mm.	6·00 mm.
Greatest pronotal width ...	1·30 mm.	1·50 mm.

6 ♂♂ (one of which the type), 6 ♀♀, Papua, Rivura, New Guinea Highlands, June 1953 (*R. Carne*). On Cinchona. The type is deposited in the British Museum (Natural History).

Differs from *Eucerocoris horvathi* Poppius (1912, Öfvers. finska. Vetensk Soc. Förh., **54,** A, 30, pp. 1–2) in colour and is smaller. In structure it differs in having the clypeus feebly prominent and not separated from the vertex by a transverse sulcus, relatively shorter antennal segments, the posterior margin of the pronotum feebly convex and not straight and the femora straight not curved.

XYLEBORUS MORSTATTI HAG. (COLEOPTERA, SCOLYTIDAE), A SHOT-HOLE BORER ATTACKING AVOCADO PEAR IN THE SEYCHELLES.

By E. S. Brown.

E.H.N.

Commonwealth Institute of Entomology.

(Plate XLIV.)

Xyleborus morstatti Hag. is well known as a pest of coffee. Hagedorn (1913) and Chevalier (1931), among others, have given accounts of its life-history and occurrence on this crop, and the latter author gave figures illustrating its boring activities. The first account known to me of the beetle attacking avocado pear (*Persea americana*) is that by Paine (1934) in Fiji. He noted that it bored into the thin green branches and also into larger woody stems, causing die-back, and in some cases threatened the death of the tree. Later, Lever (1938, 1939) gave further details, including a figure illustrating the beetle and its boring activities, and suggesting several methods for its control. The only other record of attack on avocado pear is from Mauritius (Jepson, 1939).

In the Seychelles, symptoms identical with those described by Paine and Lever were noted in one small planting of some half-dozen avocado pear trees near Port Victoria. The apical portions of several branches on five of the trees had died as the result of damage to the vascular tissues. Although no further occurrences were noted on trees examined elsewhere in the islands, and there is as yet no apparent danger of it becoming a serious pest, it is as well to put some details on record, especially as it is possible to illustrate the symptoms with photographs which will assist in recognition.

Branches up to about one inch in diameter, but usually smaller, were attacked. The entrance hole is round, and passes in at right angles to the surface as far as the central pith. The most characteristic external symptom for recognition is the appearance of a soft, white powdery material on the surface of the stem around the entrance hole (Pl. XLIV, figs. 1 & 2), which is sometimes obscured by it (Pl. XLIV, fig. 3). The powder shows no organic structure under the microscope, and has been regarded as a reaction product of the tree in response to the injury; although this appears to require proof, it is probably true, because no such product has been described when the same beetle attacks coffee and other plants (*e.g.*, Hagedorn, 1913; Chevalier, 1931). If it is brushed away and the twig is examined again after a week, more is found to have accumulated.

Usually the tunnel is simple (Pl. XLIV, fig. 4), but not infrequently it bifurcates. The end of the tunnel is enlarged to form a cavity in the pith, the lining of which becomes blackened and which may extend about half an inch up and down the stem. Brown discoloration followed by the death of the parenchyma and vascular tissues may extend further, and the whole of the distal part of the stem may die as a result. The walls of the cavity are lined with a yellowish and closely matted pad of fungal mycelium, in which oblong, stalked fruiting bodies can be distinguished under the microscope. Thin hyphae may pass across the cavity from one wall to the other.

All stages of the beetle were found in the cavities except pupae, and these also have been found by others. The eggs are sausage-shaped, whitish and translucent; they were found in six cavities examined, the number per cavity ranging from two to seven and averaging 4·3. Larvae were found in several cavities (4 to 7 in each). Adults were found in most cavities, but never more than one in each. Three cavities examined contained adults, larvae and eggs together, the maximum content for one cavity being 1 adult, 7 larvae and 2 eggs. These figures probably do not represent full-size batches, since Chevalier (1931) records 30 to 50 eggs in one gallery on coffee in West Africa, and Lever (1939) records up to 26 individuals of all stages on avocado pear in Fiji.

Associated Fungi.

Betrem (1931) states that the larvae feed solely on fungus, and that moisture is necessary and infestation is slight in the dry season in Java. It thus appears to be a true ambrosia feeder. Muller (1933) states that an ambrosia fungus of the *Monilia* type is associated with *X. morstatti* and with three other species of *Xyleborus* in the Netherlands Indies; in older galleries he records *Fusarium* also growing with the ambrosia fungus. Some infested twigs of avocado pear from the Seychelles were sent to the Commonwealth Mycological Institute, where Dr. Wiltshire kindly had the fungi isolated and identified as a mixture of *Cladosporium cladosporiodes* (Fresen) de Vries and *Penicillium pallidum* G. Smith. No other identifications of fungi appear to have been made from infestations in avocado pear; it would be interesting to know to what extent the species of fungus varies geographically, and with the host plant. Trotter (1934) has given an account of a *Monilia* type fungus infesting tunnels of *Xyleborus* in Ceylon, but does not state what species is concerned.

Hagedorn (1913) states that it is the fungus rather than the beetle which causes the major part of the damage to the plant.

Recorded Distribution.

The following is a summary of the distribution of *X. morstatti* as known at present.

WEST AFRICA: widely distributed in the tropical areas; chiefly on coffee but also on mango, cacao and *Bauhinia tomentosa*.
EAST AFRICA: on coffee, *Erythrina* and *Melia azedarach*.
MADAGASCAR: on coffee.
MAURITIUS and SEYCHELLES: on avocado pear.
INDIA (Mysore): on coffee; in summer, when it does not breed on coffee, it is said to occur on *Crotalaria* and *Clerodendron* (Anon., 1941).
INDO-CHINA: on coffee.
JAVA and SUMATRA: on coffee, oil palm (*Elaeis*), mahogany, coca (*Erythroxylon coca*), *Dendrobium veratrifolium* and *Sambucus canadensis*.
FIJI: on avocado pear. It is of interest that Lever (1939) recorded it together with the mealybug, *Icerya seychellarum* (Westw.), which was also associated with it in the Seychelles, where the ant, *Technomyrmex detorquens* (Wlk.) was tending the mealybugs. The association, however, seems to be coincidental and without any special significance.

Methods of Control.

Chevalier (1931) was only able to suggest cutting off and burning infested branches, and destroying completely all badly infested coffee bushes. While the destruction of dead wood is important, it will not rid avocado pear trees of the beetles, since many go into thicker, living branches which might be saved, and the sacrifice of whole trees is undesirable. Hagedorn (1913) suggests sticking twigs of coffee in the ground in plantations to act as traps, since he states that the beetle will not attack completely healthy wood. Lever (1938) suggests several methods designed to kill the beetle.

Control methods were not seriously investigated in the Seychelles, but the only method tried was successful enough to be put on record. The powdery exudation was brushed off in order to expose the tunnels. A 10 per cent. emulsion of Aldrex (containing 2·44 per cent. of aldrin at this dilution) was absorbed into a sponge or pad of cotton-wool, which was then pressed lightly on to the surface of the twigs at the openings of the tunnels, with the object of expelling a little emulsion which might diffuse into the tunnel. After three days a number of tunnels were cut open. Out of 10 adult beetles recovered 9 were dead, and of 16 larvae all were dead or moribund. A fortnight later the trees were treated again. Five weeks later (on 3rd January) there was very little fresh infestation, but treatment was repeated where necessary. The trees maintained a healthy appearance after this until last examined on 12th February. This treatment is only suitable for use on a limited scale since it is laborious, and would have to be modified for trial on a large scale.

Summary.

Xyleborus morstatti Hag. is a shot-hole borer which is well known as a pest of coffee. It has also been recorded from avocado pear (*Persea americana*) in Fiji, and is here reported attacking the same tree in the Seychelles, where it appears to be too scarce so far to do any serious damage.

The infestations and nature of the damage on avocado pear are described and illustrated, and the recorded geographical distribution of the insect is summarised.

A method of insecticidal control is described which, on the small scale on which it was carried out, appears to have been successful.

Acknowledgements.

I am grateful to Mr. R. D. Pope and Mr. E. A. J. Duffy, of the Commonwealth Institute of Entomology, for identification of the beetles, and to Dr. M. B. Ellis and Major H. A. Dade for identification of the fungi. To my assistant, Mr. J. Dookley, I am indebted for making treatments and examinations on occasions when I was unable to do so, and to Mr. Watters for drawing my attention to the damage and allowing me to do the experimental work on his property.

References.

ANON. (1941). Agriculture and Animal Husbandry in India in 1938–1939.—422 pp., 10 pls. Delhi.

BETREM, J. G. (1931). Een en ander over de takkenboeboek.—Bergcultures, **5,** pp. 404–409.

CHEVALIER, A. (1931). Sur un dangereux ennemi du caféier en Guinée française : le borer des rameaux (*Xyleborus morstatti* Haged.).—Rev. Bot. appl., **11,** pp. 661–665.

HAGEDORN, M. (1913). Borkenkäfer (Ipidae), welche tropische Nutzpflanzen beschädigen.—Tropenpflanzer, **17,** pp. 43–51, 99–104, 154–160, 211–216, 266–270.

JEPSON, W. F. (1939). Entomological Division.—Rep. Dep. Agric. Mauritius 1937, pp. 41–46.

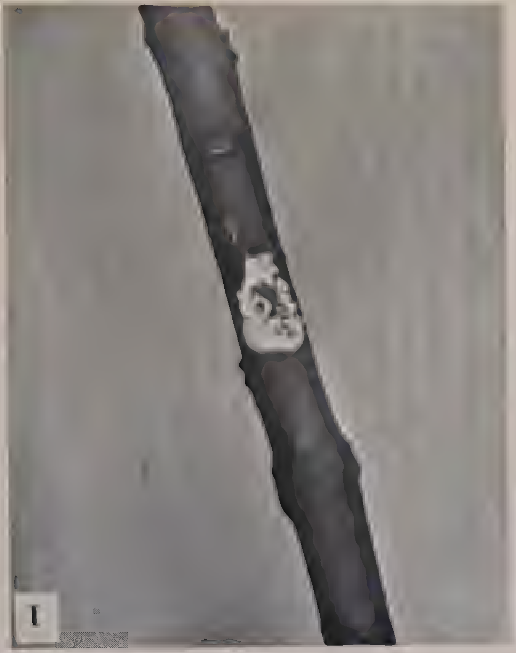
LEVER, R. J. A. W. (1938). The shot-hole beetle borer of avocado pear trees.—Agric. J. Fiji, **9,** no. 1 pp. 20–21.

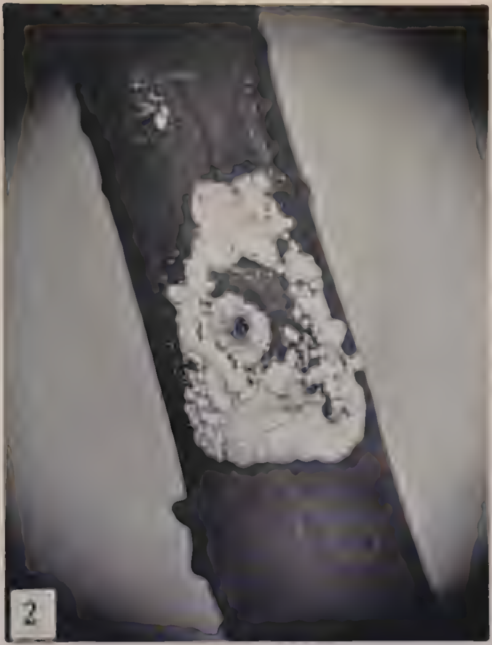
LEVER, R. J. A. W. (1939). Entomological notes.—Agric. J. Fiji, **10,** no. 1 pp. 17–20.

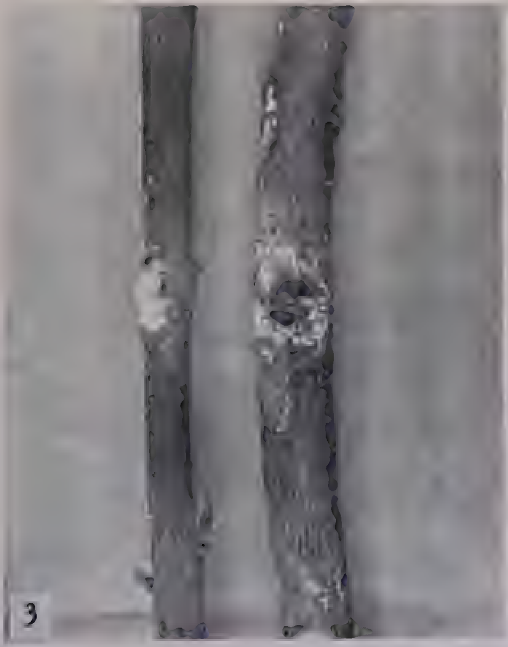
MULLER, H. R. A. (1933). Ambrosia fungi of tropical Scolytidae in pure culture.—Versl. Afd. Ned. Oost-Indië ned. ent. Ver., **1**, pp. cv–cvii, cxxv.

PAINE R. W. (1934). Entomological notes.—Agric. J. Fiji, **7**, no. 1 pp. 39–41.

TROTTER, A. (1934). Il fungo-Ambrosia delle gallerie di un Xyleborino di Ceylon. —Ann. Ist. sup. agr. Portici, (3) **6**, pp. 256–275.







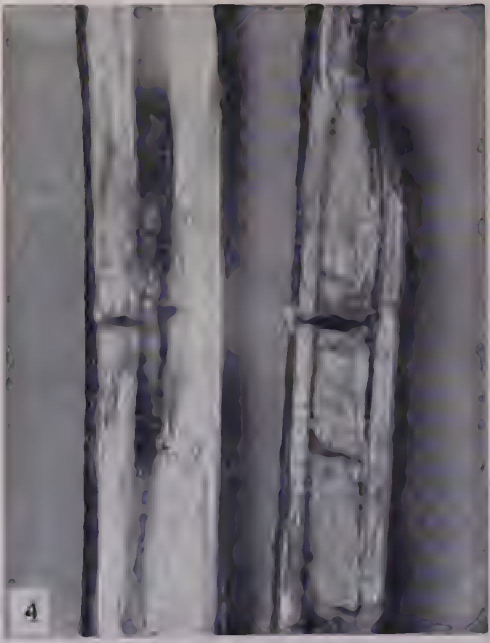


Fig. 1. Twig of avocado pear (*Persea americana*) with entry hole of shot-hole borer, *Xyleborus morstatti* Hag. Note the characteristic exudation of white powdery material surrounding the hole. (Natural size.)

Fig. 2. The same enlarged. (×3.)

Fig. 3. Twigs of avocado pear attacked by *X. morstatti*, showing variation in quantity and extent of the white exudation. (Natural size.)

Fig. 4. Twigs of avocado pear cut in section longitudinally, showing galleries bored by *X. morstatti*. Note the decomposition extending upwards and downwards through the host tissues from the gallery. (×2.)

STUDIES CONCERNING THE UPTAKE OF CONTACT INSECTICIDES.

I.—THE ANATOMY OF THE TARSI OF CERTAIN DIPTERA OF MEDICAL IMPORTANCE.

By C. T. Lewis.
Imperial College Field Station, Sunninghill, Berks.

The tarsi of Muscid and Tachinid flies, in addition to their intrinsic interest as highly specialised organs of locomotion and perception, are directly concerned in the mode of action of insecticidal deposits. Exposed flies pick up particles from a deposit primarily upon the ventral tarsal spines and on the pretarsi, and, in spite of cleaning reflexes, an appreciable quantity of material can be retained by the tarsi for some hours after exposure (Lewis & Hughes, unpublished). Particular regions of the tarsi (*e.g.*, pulvilli, joints, chemoreceptors) are of special interest as possible preferred sites of penetration of insecticide, though there is very little information available on this subject, and the structure of the regions concerned has been imperfectly understood. A knowledge of the anatomy of the tarsi appears to be essential to the understanding of the accumulation and penetration of contact insecticidal deposits.

No full description of the anatomy of the tarsi of any species of Diptera has been published, but comparative accounts of certain details of the tarsal structure of *Musca domestica* L. and of species of other Orders have been given by Hayes & Liu (1947) and Sarkaria & Patton (1949). These two accounts were principally concerned with the setae presumed to be chemoreceptors and with the pulvilli, respectively. In the present work, additional evidence concerning the structure of these organs has been obtained and particular attention has been paid to (1) the external morphology, to which is related the accumulation and retention of material from deposits, (2) the variations in cuticular structure, which possibly affect the rate of penetration of contact insecticides, (3) the sense organs and the distribution of tarsal nerves, since several of the more commonly used insecticides are considered to be nerve poisons (*e.g.*, DDT, pyrethrum, BHC).

Methods.

Whole mounts, dissections and stained serial sections of the tarsi of the blowfly (*Phormia* (*Protophormia*) *terraenovae* (R.-D.)), the tsetse fly (*Glossina palpalis* (R.-D.)) and the house-fly (*Musca domestica* L.) were prepared for examination. Tarsi to be sectioned were fixed in Bouin's solution and impregnated by Petterfi's Celloidin-paraffin method. The silver staining technique of Romanes (1950) was found to be the best of several staining methods which were tried. This method gave an exceedingly clear definition of nerve fibres and sensillae. Chlorazol Black, Heidenhain's haematoxylin and Mallory's triple stain were also used.

Phormia (Protophormia) terraenovae.

Tarsal segments and setae.

The three pairs of tarsi differ slightly in form and function and the individual segments vary considerably in length (see below and Table I), but the large numbers of setae present are distributed in a single pattern common to all segments (fig. 1).

This pattern consists of:

1. Large primary spines on which the fly walks.
2. Two closely packed ventral rows of receptors which brush the surface at their tips.
3. Secondary spines which protect the ventral receptors from mechanical damage.
4. A small number of dorsal receptors.
5. Dorsal and lateral rows of bristles.

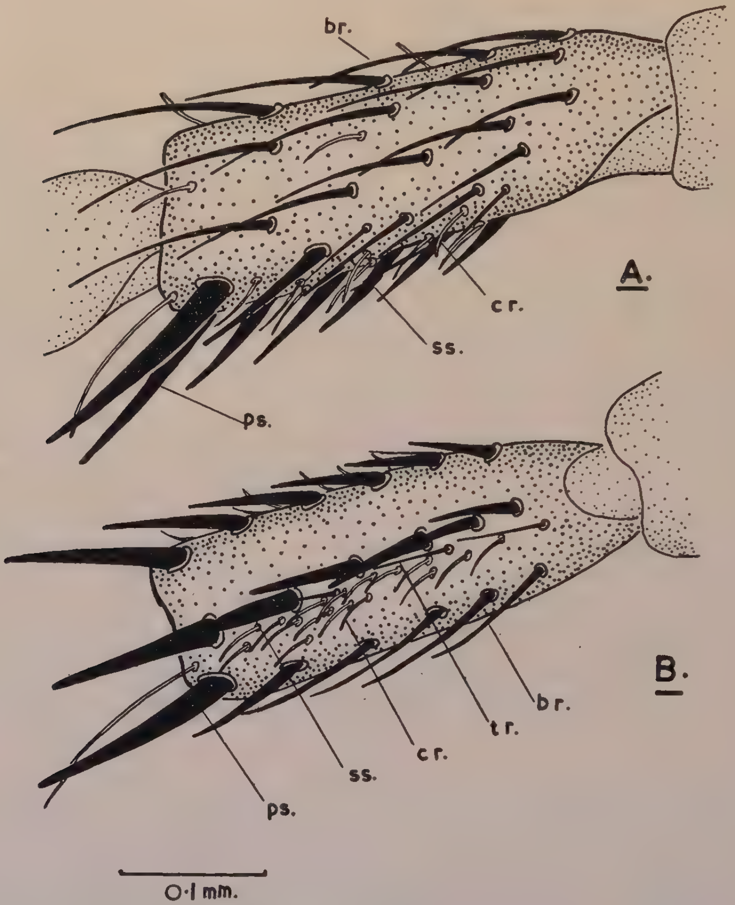


Fig. 1.—Third tarsal segment of *Phormia terraenovae*: (A) lateral view; (B) latero-ventral view; *br.*, bristle; *ps.*, primary spine; *ss.*, secondary spine; *cr.*, chemoreceptor; *tr.*, fine tactile receptor.

Primary tarsal spines occur in pairs at the ventral and latero-ventral extremities of each segment except the last, projecting below the intersegmental joints. Traces made by walking flies on smoked surfaces demonstrate that these large spines are the points of contact with which the tarsi engage a level surface; they carry the weight and transmit the propulsive forces involved in a fly's movements. Each primary spine is innervated by a fibre from a bipolar nerve cell.

The smaller *secondary tarsal spines* are located in two ventral rows and clearly protect the adjacent delicate receptors, which, but for the spines, would be subjected to pressure against irregularities of the substrate. When a fly walks over a perfectly smooth surface, the secondary spines do not make contact. They are also innervated by fibres from bipolar nerve cells.

Bristles, similar to those covering the thorax and abdomen of this fly, occur in several rows over the dorsal and lateral surfaces of each segment. They are not associated with nerve endings. Their flexibility may enable them to protect the thin inflexible integument against chance hazards.

In addition to the above sets of setae, the first segments of the fore and hind tarsi only are equipped with large numbers of short, straight, ventral bristles which are not innervated. These may play an important part in the accumulation of particles from a deposit.

The *microtrichia* covering the tarsal cuticle are hollow outgrowths from the surface, twenty to thirty microns long, spaced at intervals of ten microns or less. The hollow tenent hairs of the pulvilli may be considered to be modified microtrichia.

The chemoreceptors.—Although the tarsal gustatory sense of blowflies has been extensively investigated by experimental methods, comparatively little information is available concerning the structure of the contact chemoreceptors. The subject has been reviewed by Dethier & Chadwick (1948) and by Frings & Frings (1949). Tinbergen (1939) has described hollow setae, each containing an eccentric chitinous partition, distributed in the chemoreceptive regions of *Calliphora erythrocephala* (Mg.). These setae are probably analogous to the contact chemoreceptors of the tarsi of *P. terraenovae*, which are hollow setae faced with an exceedingly delicate membrane less than one micron thick and are characteristically innervated by a spindle-shaped group of sensory neurocytes (fig. 2) (*cf.*, Lewis, 1954). Each fly possesses over one thousand receptors of this type, 95 per cent. of which are located in two ventral rows on the tarsal segments. The remainder are distributed dorsally. Details of the distribution of receptors are presented in

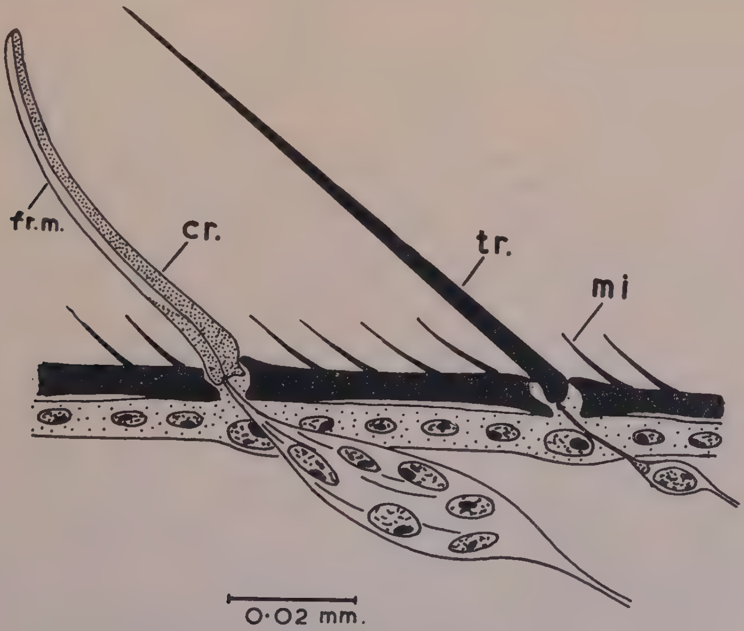


Fig. 2.—Tarsal sense organs of *Phormia terraenovae*: *cr.*, chemoreceptor; *fr.m.*, frontal membrane; *mi.*, microtrichia; *tr.*, tactile receptor.

Table I. It will be seen that the short fore-tarsi are the most sensitive and that the receptors are most densely packed on the second, third and fourth segments. Most of the receptors are 40 to 60 microns in length but longer receptors (150 to 250 microns) are found at the distal extremity of each segment and at the proximal end of the first segments of the fore-tarsi.

The setae described above were positively identified as chemoreceptors by experiments in which individual setae were stimulated. Newly emerged flies were starved for eight days, after which they were fastened by the dorsal thorax to waxed glass slides. The following day the fore-tarsi of fifty surviving flies were precisely stimulated under a high power dissecting microscope by glass fibres wetted with 10 per cent. sucrose solution. When a whole tarsus was touched with 10 per cent. sucrose solution, 90 per cent. of the flies extruded the proboscis; when 40 receptors in two ventral rows were touched, 50 per cent. of the flies responded; when 20 receptors were stimulated 20 per cent. of the flies responded. No response to sucrose was obtained when only one receptor on each fly was touched, and no response to sucrose was obtained at any part of the tarsus from which receptors were absent. No response was obtained when the receptors were touched with clean dry glass fibres. These experiments demonstrated that the receptors were gustatory end organs and that stimulation of a number of receptors was necessary to excite a positive feeding response in starved flies.

The frontal membrane (see fig. 2) is probably the boundary across which stimulating substances enter a receptor. The nature of the membrane was briefly investigated to determine whether a lipoid epicuticle was present, in view

TABLE I.

Distribution of tarsal chemoreceptors and nerve supply of *Phormia terraenovae*.

Tarsus	Segment	Length (mm.)	Total no. chemoreceptors	Cross-sectional area of nerves entering segments
Fore ..	1	0·87	52	222 sq. microns
	2	0·38	56	164
	3	0·35	48	81·5
	4	0·27	42	55
	5	0·32	34	38
Total ..		2·19	232	
Mid	1	1·11	38	154
	2	0·48	40	106
	3	0·36	30	63·4
	4	0·32	24	38·4
	5	0·38	20	30
Total ..		2·65	152	
Hind ..	1	1·15	38	164
	2	0·54	34	106
	3	0·41	26	66·5
	4	0·32	22	38·4
	5	0·39	20	22·8
Total ..		2·81	140	

Average for five individuals. The distribution is the same for both sexes. No nerves enter the pretarsi.

of the fact, first observed by Minnich (1926), that aqueous solutions and water can be perceived by the tarsal taste sense of blowflies. The contact angles of fine droplets of distilled water, precipitated on to chilled tarsi by the process of dew formation, were found to be the same (95°–100°) on the frontal membranes of chemoreceptors as elsewhere on the tarsal integument. Similarly the contact angles of acetic acid droplets, also precipitated from the vapour phase, were the same (70°) at the frontal membrane as elsewhere, though after two minutes the contact angle fell owing to the action of acetic acid on the cuticle surface.

When insects are immersed in mineral oils, water droplets are slowly exuded (Wigglesworth, 1942). The oil presumably disturbs the lipoid epicuticle separating the aqueous biophase from the exterior. When the tarsi were placed in xylene, kerosene or liquid paraffin, the time lag before the formation of visible droplets at the frontal membrane was the same as elsewhere on the tarsal integument. These observations demonstrate that the frontal membrane is not more easily wetted than the normal cuticle surface, and that water does not pass outwards more readily across the membrane than across other regions of the cuticle, being hindered by a barrier which can be dispersed by oils. The evidence suggests that a normal lipoid epicuticle may form part of the structure of the receptor surface, and this view is supported by the observation that the stimulating powers of a wide range of aqueous solutions of inorganic electrolytes and of organic substances appear to be related to lipoid solubility or to oil-water distribution coefficients (Dethier & Chadwick, 1948).

Tactile receptors.—Nerve endings from bipolar sense cells are associated with the primary and secondary tarsal spines, which must therefore be considered tactile. In addition, hinged setae which are too fine to have a mechanical function are distributed among the ventral rows of chemoreceptors (figs. 1 & 2). These are also supplied with bipolar sense cells.

Pumphrey (1936) demonstrated that the stimulation of fine hairs and stout spines on the tibia of the cockroach produced impulses in the sensory nerves which respectively resembled those of touch receptors and proprioceptors of vertebrates. It is possible that the innervated stout spines and fine hairs of the tarsi of *P. terraenovae* may also produce different responses to tactile stimuli.

The intersegmental joints.

The tarsal segments articulate dorsally about elaborate monocondylic joints (fig. 3). A deeply sculptured elliptical condyle moves in a hemispherical socket, and a flexible collar of endocuticle unites the neck of the condyle to the zone of the socket. The collar is pierced by a row of slots which increase its flexibility, and is folded to allow for extension during movement of the condyle.

The articulation occupies the dorsal intersegmental region; ventrally the segments are directly connected by a flexible unsclerotised membrane. Through the foramen bounded by this membrane pass the tissues, including nerves, circulation membrane, tracheae and unguitractoral apodeme.

The pretarsi.

The sclerotic components of the pretarsus (the claws, basipulvilli and flexor plate) are linked to each other and to the last tarsal segment by a transparent flexor membrane. The paired claws and basipulvilli pivot upon a median recurved lip or tuberculum formed by the dorsal extremity of the last tarsal segment. The unguitractoral or flexor plate, a flat ventral structure prolonged into a spinous empodium, is connected to muscles in the tibia by a long apodeme. When the plate is drawn back by the tibial muscles, the attached flexor membrane pulls the claws and pulvilli downwards to engage the surface. Flexion of the pretarsus is thus a muscular process, while a return to the normal extended position is brought about by the elasticity of the thick endocuticle attaching the articulating parts to the tuberculum. This mechanism can be demonstrated by the manipulation of a detached tarsus and pretarsus. The pulvilli extend from the basipulvilli as distensible sacs of endocuticle supported by radiating sclerotised ridges inset in the dorsal wall. The fine tenent hairs covering the ventral surfaces of the pulvilli are not associated with glandular cells (*cf.*, the adhesive organs of species in other Orders, *e.g.*, *Rhodnius prolixus* Stål (Gillett & Wigglesworth, 1932)). It appears that a lymph may saturate the gelatinous interior of the pulvilli and be drawn into the tenent hairs by capillary forces. When the pulvilli are pressed on to a surface, a small quantity of fluid is expressed from the tenent hairs and this increases the adhesion of the organs to the surface.

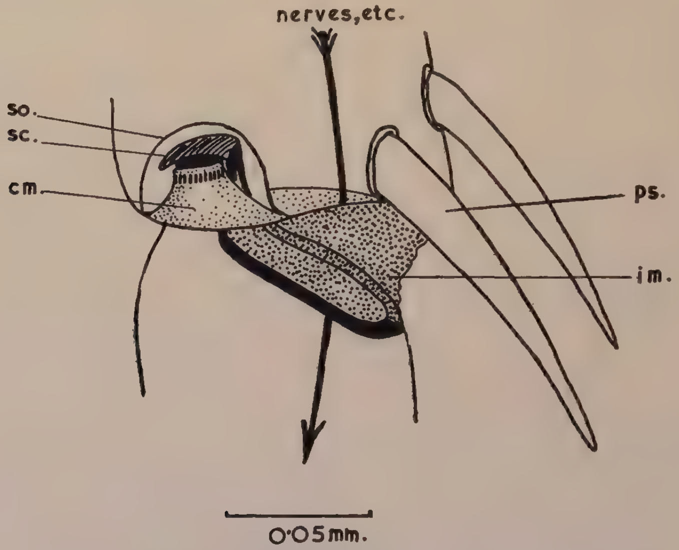


Fig. 3.—Intersegmental joint of *Phormia terraenovae*, lateral view, diagrammatic: *cm.*, collar membrane; *im.*, ventral intersegmental membrane; *ps.*, primary spine; *sc.*, sculptured condyle; *so.*, joint socket.

The pulvillus is filled with a clear gelatinous substance which contains no nuclei and is quite different in appearance from the granular cytoplasm of hypodermal cells in the pretarsus. Like the normal endocuticle elsewhere, the interior of the pulvillus is stained blue by Mallory's triple stain, while hypodermal cells in the basipulvilli are stained pink. Fragments of the interior of the pulvilli surviving hot KOH treatment respond positively to the chitosan test, indicating the presence of chitin. There is therefore no doubt that the viscous substance filling the pulvilli consists of endocuticular material secreted by an underlying layer of large hypodermal cells situated at the junction of the pulvilli and the basipulvilli (fig. 4 C). Slifer (1950) has described the thick endocuticle of the pliant sole of the arolia and euplantulae of ACRIDIDAE (Orthoptera), which consist largely of rods embedded in a fluid. It seems that this may provide an analogous example of a viscous chitinous medium within a flexible organ.

The above account, which applies also to the pretarsi of *G. palpalis* and *M. domestica*, differs in several important respects from earlier accounts of the pretarsi of *M. domestica*. The dorsal sclerotised ridges were interpreted by Hayes & Liu (1947) as a system of internal canals. There is, however, no doubt that the structures form rigid superficial corrugations in the dorsal wall which strengthen the soft pulvillus, as Sarkaria & Patton (1949) have also emphasised.

The interior of the pulvillus was considered by Sarkaria & Patton (*loc. cit.*) to consist of a single large cell. The histological evidence detailed above clearly indicates that the interior consists of soft endocuticle, not cytoplasm. The latter authors also described and illustrated large bundles of fibres passing from cells in the last tarsal segment into the pulvilli; these, it was stated, were apparently sensory nerve fibres, though the location of any peripheral endings of the fibres was not described. The existence of such fibres was not confirmed in the present investigation, during which several dozen tarsi were sectioned and stained. In no case were nerve fibres observed in any part of the pretarsi, nor were any sense organs found which could account for the presence of nerves.

To sum up, the pulvilli were found to consist entirely of soft cuticle secreted by hypodermal cells located at the extremity of the basipulvilli. No nerves, sense organs or gland cells were found associated with the pulvilli.

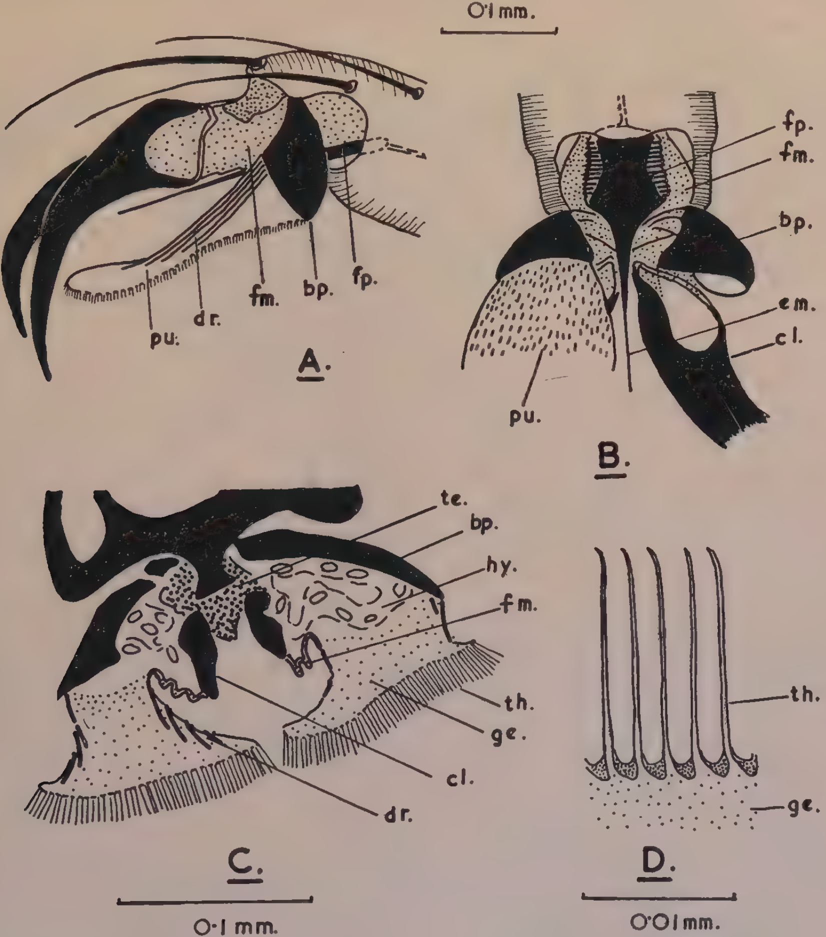


Fig. 4.—Pretarsus of *Phormia terraenovae*: (A) lateral view; (B) ventral view of same, with one pulvillus removed; (C) pretarsus of *Glossina palpalis*, frontal oblique section; (D) pulvillus of *Glossina palpalis*, detail of sole: *bp.*, basipulvillus; *cl.*, claw; *dr.*, dorsal ridges; *em.*, empodium; *fm.*, flexor membrane; *fp.*, flexor plate; *ge.*, gelatinous endocuticle; *hy.*, hypodermal cells; *pu.*, pulvillus; *te.*, thick endocuticle; *th.*, tenent hairs. Endocuticle is stippled throughout.

Internal anatomy of the tarsi.

The hypodermis consists of a single layer of cells between which no cell boundaries can be distinguished. A basement membrane is present. Associated with the normal hypodermal cells are the trichogen and tormagen cells of setae, the spindle-shaped groups of chemosensillae cells and the subepidermal bipolar cells of tactile sensillae. Multipolar nerve cells with free endings among the hypodermal cells could not be found, although sensory nerve cells of this more primitive type have been described in association with the leg joints of *Aeshna* nymphs (Odonata) (Zawarzin, 1912).

The tracheal trunks are closely associated with the main nerves of the tarsi. A circulation membrane of connective tissue passes through each tarsus, dividing the haemolymph into ventral and dorsal sinuses. The membrane is held in place by median ventral groups of six small apodemes at the distal end of each segment.

The histology of the pulvilli has been described above.

Musca domestica.

The tarsal setae and receptors of *M. domestica* are shorter and more densely crowded than those of *P. terraenovae*, but they are distributed in a similar pattern. The house-fly possesses more than one thousand tarsal chemoreceptors (Table II) each differentiated longitudinally into a thin frontal membrane and a thicker, opaque posterior wall. Hayes & Liu (1947) have stated that no chemoreceptors are present on the first tarsal segments of the tarsi of *M. domestica*; the statement was not confirmed in the present investigation, for more than two hundred chemoreceptors were counted at this location on each fly. The pulvilli are

TABLE II.

Distribution of tarsal chemoreceptors of *Glossina palpalis* and *Musca domestica*.

Tarsus	Segment	No. of chemoreceptors, *G. palpalis*	No. of chemoreceptors, *M. domestica*	Nerve diameter, *M. domestica*
Fore ..	1	28	58	13·5 microns
	2	16	66	
	3	14	58	
	4	12	46	
	5	8	38	
Total ..		78	266	
Mid	1	20	32	10·5
	2	14	38	
	3	14	36	
	4	12	36	
	5	8	26	
Total ..		68	168	
Hind	1	20	30	10·5
	2	14	26	
	3	14	32	
	4	12	26	
	5	8	20	
Total		68	134	

Average for 5 individuals.

filled with viscous endocuticle and are not innervated. The intersegmental joints and the internal anatomy do not differ significantly from the corresponding structure described for *P. terraenovae*.

In brief, there are no important differences in structure between the tarsi of *M. domestica* and the tarsi of *P. terraenovae*.

Glossina palpalis.

The anatomy of the tarsi of this species is also basically similar to that of the tarsi of *P. terraenovae*. There are fewer setae and receptors but the pattern of distribution is the same. In addition to the usual spines, bristles and receptors, the tarsal segments of *G. palpalis* are armoured with rows of short, stout, slotted cuticular outgrowths characteristic of the genus (fig. 5).

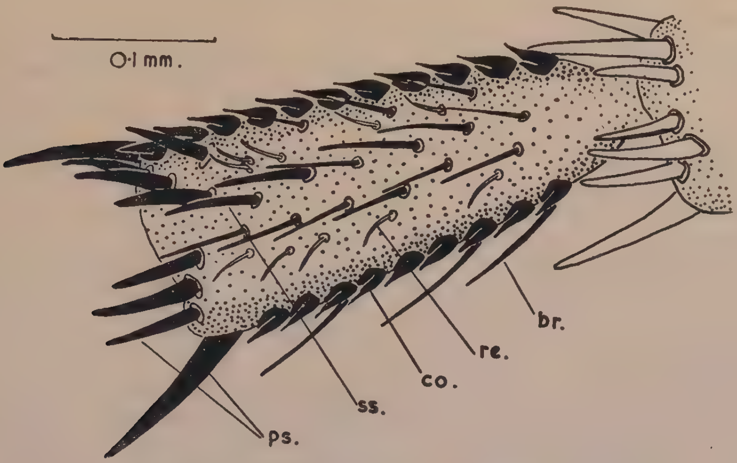


Fig. 5.—Third tarsal segment of *Glossina palpalis*, ventral view: *br.*, bristle; *co.*, slotted cuticular outgrowths; *ps.*, primary spine; *ss.*, secondary spine; *re.*, receptor, probably chemoreceptor.

Approximately four hundred tarsal receptors occur ventrally (Table II), each possessing a minute frontal membrane and innervated by a spindle-shaped group of sense cells. There seems little doubt that they are homologous to the chemoreceptors of blowfly and house-fly tarsi, though a tarsal gustatory sense has not been reported in *Glossina* spp.

The pretarsi, the intersegmental joints and the internal anatomy are all very similar to the corresponding structures described for *P. terraenovae*.

Discussion.

Walking movements and accumulation from deposits.

In the species studied, the short fore-tarsi differ from the middle and hind tarsi in the possession of many more sense organs (Table I) and comparatively small primary spines. They appear to function primarily as organs of perception, exploring the quality of the surface in advance of the mouthparts; they play only a minor part in propelling the fly, since the small primary spines are directed forward and cannot provide a grip for traction. The claws and pulvilli are the only tractive structures of the fore-tarsi. In contrast, the thrusts on the middle and hind legs of a walking fly act through the primary spines of each tarsal segment. These spines are very much longer than the ineffective spines of the fore-tarsi.

Experiments on the contamination of blowflies exposed to particulate deposits have shown that the hind tarsi collect particles more efficiently than others, possibly because a stronger propulsive thrust during walking movements increases the pressure on the deposit (Lewis & Hughes, unpublished). The first tarsal segments, which are the most hairy, can pick up more than the other individual segments or the pulvilli. Particles adhere to the ventral spines and receptors and work down to their bases and to the microtrichia. The closely packed microtrichia prevent particles 10 microns or more in diameter from making contact with the general cuticle surface, and so effectively reduce the area of contact across which insecticide particles can penetrate. The frontal membranes of chemoreceptors are readily contaminated, but the lateral and dorsal bristles play no part in the accumulation of material from a deposit.

Possible preferred sites of penetration of contact insecticide.

It is known that the toxicity of DDT varies with the *locus* of application to an insect, *e.g.*, Lindquist & others (1951) working with a resistant strain of house-flies, demonstrated that DDT picked up from a dry deposit was lethal in considerably smaller quantities than DDT entering from topical applications to the dorsal thorax. Variations in toxicity at different parts of an insect may be due to local variations in the rate of penetration of the cuticle or to differences in susceptibility of the tissues underlying the different sites of penetration, or to a combination of both factors.

Certain regions of the integument may be more permeable to DDT than others. Wigglesworth (1942) has demonstrated that the thickness of the endocuticle affects the rate of penetration of pyrethrum in oil into *Rhodnius prolixus*, while Wiesmann (1946) has suggested that sclerotin may act as a barrier to DDT penetration, though this has yet to be proved. An exocuticle is lacking at the following parts of the tarsi:

(1) the pulvilli and pretarsal flexor membrane, (2) the ventral intersegmental membranes, (3) the articulating membranes of hinged setae, (4) the frontal membranes of the chemoreceptors.

All these specialised regions of the cuticle are ventrally located, and therefore exposed to insecticide accumulated from deposits. Of these special sites the pulvilli appear to be the least important, because of the remoteness of nerve axons and because of the bulk of viscous endocuticle through which the insecticide must diffuse to reach the tissues. This view receives support from the observation of Fisher (1952) that topical treatments of DDT in benzene applied to the pulvilli are less toxic than those applied to the proximal tarsal segments. Thus the suggestion that the susceptibility of species to DDT might be correlated with the degree of development of the pulvilli (Potts & Vanderplank, 1945) appears to be unfounded.

Two tarsal trunk nerves pass close to the ventral intersegmental membranes, and nerve endings are associated with the chemoreceptors and the articulating membranes of ventral tarsal spines. These unsclerotised areas may thus be important sites of penetration to the nervous system, but little experimental evidence is yet available. In *Rhodnius* nymphs, but not adults, oily solutions of pyrethrum applied to the abdomen penetrated most rapidly around the bristles (Wigglesworth, 1942). If thickness of cuticle is the principal factor affecting the rate of entry of contact insecticides, the extremely thin lipophilic frontal membranes of chemoreceptors may be the sites of most rapid entry into the tarsi of flies.

Relative toxicity and distribution of sensory nerves.

The observations of Fisher (1952) may be interpreted as evidence that DDT acts within a very limited distance of the site of penetration. When small measured doses of DDT in benzene were applied to particular parts of house-flies, significant differences were observed between the toxicities at different locations. Topical treatments of the head were more toxic than treatments of the fore-leg, which in turn were more toxic than treatments of the middle or hind leg; also, treatments applied to the first tarsal segments were more toxic than treatments of the second tarsal segments, which were in turn more toxic than treatments of the more distal tarsal segments or the pulvilli.

It will be seen that these results may indicate a correlation between relative toxicity and the number of sensory nerve fibres present near the various *loci* of treatment. The number of sensory nerve axons, which is proportional to the number of sense organs served, is greater in each fore-leg than in the middle and hind legs, and diminishes distally in each tarsus (Tables I & II). It appears that the gradient of susceptibility postulated by Fisher from his results may well be an expression of the number of sensory nerve fibres present at different parts of the body. Moreover, the fact that the first tarsal segments are more susceptible than the second segments in spite of the greater density of receptors possessed by the latter, indicates that the number of sensory end organs affected is less important than the number of sensory nerve axons adjacent to the area of treatment.

Since the relative toxicity of DDT treatments varies over short distances and can be correlated with the number of sensory nerve fibres adjacent to the treatment, it follows that transport of toxicant away from the site of penetration is a relatively slow process. Further information relevant to this subject will be described in a later paper in this series, in which measurements of the rate of penetration of DDT solutions into structurally different regions of the integument of *P. terraenovae* will be presented.

Summary.

The anatomy of the tarsi and pretarsi of *Phormia* (*Protophormia*) *terraenovae* (R.-D.), *Glossina palpalis* (R.-D.) and *Musca domestica* L. is described, with particular reference to structures possibly concerned in the action of deposits of contact insecticides. The numerous setae which cover the tarsal segments are distributed in a pattern which is common to all three species. Long spines situated at the distal extremity of each segment are the points of contact with which a fly engages a surface, and which take the thrust as the fly walks. Proximal to the primary spines are two ventral rows of chemoreceptors, protected from mechanical damage by smaller spines. In addition there are lateral and dorsal rows of bristles.

Contact chemoreceptors, which have been identified by experiment, are present in large numbers on the tarsi of *P. terraenovae* and *M. domestica*. Each chemoreceptor is a differentiated hollow seta possessing an extremely thin frontal membrane of cuticle, in which a lipoid layer appears to be incorporated and through which a lipoid-soluble insecticide might readily penetrate to the sensory neurocytes.

Receptors of this type are also present on the tarsi of *G. palpalis*, though tsetse flies have not been reported to possess a tarsal gustatory sense.

The pulvilli of all three species are entirely filled with viscous endocuticle and possess neither nerves, sense organs nor gland cells. The pulvilli are probably less important sites of penetration of insecticide from deposits than are the tarsal chemoreceptors, articulating membranes of setae, and intersegmental joint membranes.

Measurements of nerve diameters at different parts of the tarsi are used to interpret the results of Fisher (1952) concerning the action of DDT applied to limited areas of *M. domestica*. It is concluded that the relative toxicity of DDT at different parts of the body may be correlated with the number of sensory

nerve fibres passing close to the site of penetration, but not with the number of sensory end organs directly affected.

Acknowledgements.

I am indebted to Emeritus Professor J. W. Munro, in whose Department this work was conducted, for his interest in its progress, and to Dr. A. B. P. Page for encouragement and useful criticisms. The work forms part of a research programme approved by the Colonial Insecticides Committee and financed by the Colonial Office.

References.

Dethier, V. G. & Chadwick, L. E. (1948). Physiol. Rev., **28,** pp. 220–254.

Fisher, R. W. (1952). Canad. J. Zool., **30,** pp. 254–266.

Frings, H. & Frings, M. (1949). Amer. Midl. Nat., **41,** pp. 602–658.

Gillett, J. D. & Wigglesworth, V. B. (1932). Proc. roy. Soc., (B) **111,** pp. 364–376.

Hayes, W. P. & Liu, Yu-su. (1947). Ann. ent. Soc. Amer., **40,** pp. 401–416.

Lewis, C. T. (1954). Nature, Lond., **173,** p. 130.

Lindquist, A. W., Roth, A. R., Yates, W. W., Hoffman, R. A. & Butts, J. S. (1951). J. econ. Ent., **44,** pp. 167–172.

Minnich, D. E. (1926). Biol. Bull., Wood's Hole, **51,** pp. 166–178.

Potts, W. H. & Vanderplank, F. L. (1945). Nature, Lond., **156,** p. 112.

Pumphrey, R. J. (1936). J. Physiol., **87,** p. 15.

Romanes, G. J. (1950). J. Anat., **84,** pp. 104–113.

Sarkaria, D. S. & Patton, R. L. (1949). Trans. Amer. ent. Soc., **75,** pp. 71–82.

Slifer, E. H. (1950). Ann. ent. Soc. Amer., **43,** pp. 173–188.

Tinbergen, L. (1939). Arch. néerl. Zool., **4,** pp. 81–92.

Wiesmann, R. (1946). Verh. schweiz. naturf. Ges., **126,** pp. 166–167.

Wigglesworth, V. B. (1942). Bull. ent. Res., **33,** pp. 205–218.

Zawarzin, A. (1912). Z. wiss. Zool., **100,** pp. 245–286.

FIELD OBSERVATIONS ON THE CACAO MIRIDS, *SAHLBERGELLA SINGULARIS* HAGL. AND *DISTANTIELLA THEOBROMA* (DIST.), IN THE GOLD COAST.

PART III. POPULATION FLUCTUATIONS.

By G. Williams, B.Sc.

The Zoology Department, The University, Reading.

E.M.N.

This is the final part of the series which aims at summarising our present knowledge of the biology of the two species of Mirids, *Sahlbergella singularis* Hagl. and *Distantiella theobroma* (Dist.), which are important pests of cacao (*Theobroma cacao*) in West Africa. The investigations have been made mainly by field observations and the sampling methods used, indicated in the present text by the use of capital initial letters, have been fully described in Part I (Williams, 1953*a*). Part I was a discussion of the factors determining the distribution and appearance of Mirid damage in the field; Part II (Williams, 1953*b*) was a comparison of the habits of the two species; the present part is an account of the population fluctuations and a consideration of some of the factors which are of importance in the natural control of cacao Mirid populations.

Annual Population Changes.

The major changes in Mirid population throughout the year are manifest without the need for counts. Toward the end of the dry season (March and April) the bugs appear to be completely absent, becoming conspicuous on pods during the later part of the fruiting season in November and December. Their presence on stems is shown by the death of attacked chupons and fans in the middle of the dry season (January and February), the death of the fan tips of the canopy presenting the symptom described as seasonal blast.

The general change in numbers is sufficiently great to be expressed in the simplest of the sampling techniques, the Routine Collections, and fig. 1 shows the mean number of *S. singularis* per 100 trees for each month during the first two years of sampling, from August 1944 to July 1946 inclusive. In fig. 1 the total count of *S. singularis* has been divided to show the part of the plant, pod or stem, from which the bugs were collected. The counts confirm the general impression of population change. From April to July inclusive, there were less than 20 *S. singularis* per 100 trees in contrast to the November to January period when the number was never below 60, and rose to as many as 109 *S. singularis* per 100 trees. In more detail, there was a steady increase in the number of bugs on pods from July onward, an increase associated with the increasing number of pods available, but lagging behind in time. From November there was a rapid fall in the number of bugs on pods, for, as pods ripen they become less suitable for Mirid development and are completely removed during harvest. Associated with the multiplication of bugs on pods there was also an increase in numbers on stems, an increase which followed the pod-population curve in 1944 but which was simultaneous with the pod-population curve in 1945. The total population of *S. singularis* did not fall with the population on pods after November but continued to a second maximum in February, after which there was an abrupt drop to the low numbers of the late dry season and early rainy season.

Such a sequence agrees well with the general course of fluctuations of *S. singularis*, in West Africa as a whole, as described by Squire (1947), who concluded that the increase in Mirid populations was dependent upon the "edaphic factor of fruiting", the influence of climatic changes being slight in comparison. The Tafo curves may be similarly interpreted as an initial increase occasioned by the presence of pods, the large population built up in this way transferring to stems when pods are no longer available. The sudden fall in numbers, on the other hand, Squire attributed directly to the climatic rigours of the dry season. The adverse effect of the dry season is illustrated by the restricted habitat of the bugs at this time, for they are found only on chupons of a very definite type. These are chupons (about as thick as one's finger) that do not wilt rapidly under the combined effect of Mirid attack and dry surroundings, yet are not so hard and woody as to prevent the bugs feeding.

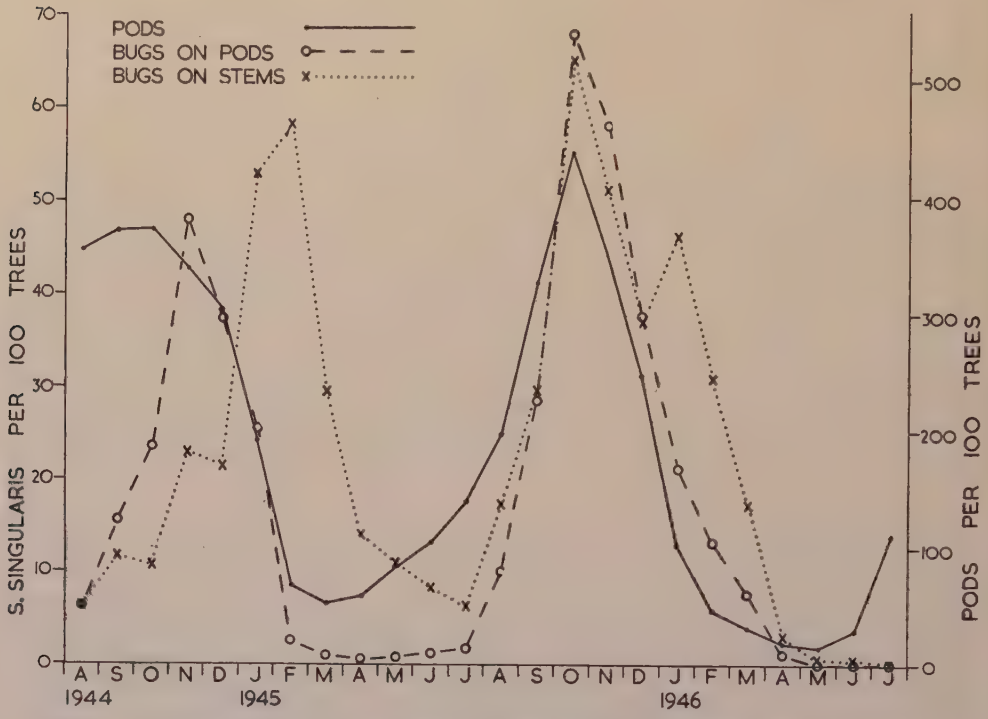


Fig. 1.—Fluctuations in the mean monthly population of *S. singularis* per 100 trees as estimated during the first two years of the Routine Collections.

Examination of the data and illustrations given by Squire (1947) shows the relationship between the fruiting season and Mirid numbers as he suggests, but it also shows that the fruiting period is itself related to climatic factors, particularly rainfall. It is not certain, therefore, whether the observed relation between pods and Mirid numbers is one of cause and effect as claimed by Squire or whether both are the result of some common factor such as climate. If numbers of pods were the main determinant of population increase it would be expected that some clear relationship should be demonstrable between the number of pods, the number of Mirids on pods and the resultant later peak in the number of Mirids on stems. The Observation Plots, which were examined at fortnightly intervals, covered a wide range of cacao, but no such relationship was apparent in them. In fig. 2 the changes in the population of *S. singularis* in four of the plots are illustrated. These four have been chosen because they are paired plots, *i.e.*, a plot in a pocket is very close to a plot in healthy cacao, but consideration of all the plots does not alter the findings. The B plots of fig. 2 were both in young cacao which was just coming into bearing, and the F plots were in mature cacao. B " Healthy " was laid out in cacao which was healthy at the time, but which suffered from blast in the early months of 1947 and continued subsequently as an area of light blast. F " Healthy " remained healthy throughout the period of sampling but, unfortunately, was only a small plot comprising 48 trees as opposed to the 152 in F " Pocket ", 152 in B " Pocket " and 157 in B " Healthy ". The curves of fig. 2 show, in a general way, the features of the annual cycle noted in the Routine Collections; all, except F " Healthy " which possessed few chupons suitable for Mirids, show the characteristic fall in numbers during the first quarter followed by the increase in the numbers of pods and bugs on pods. The stem population may be interpreted as bimodal, with the first peak coinciding with the maximum numbers on pods and the second after the harvesting period. Clearly, the presence of Mirids on pods will depend on there being some pods present, but beyond that there is no necessary increase as the number of pods increases; the maximum number on pods is about the same for B " Healthy " as for F " Healthy " despite the fact that there were nearly five times as many pods per 100 trees in F as in B at their respective peaks; similarly, F " Pocket ", with only one-third the peak number of pods of F " Healthy ", had 12 times as many *S. singularis* on pods. Nor is there any relationship between the number of bugs on pods and the number on stems at the later peak.

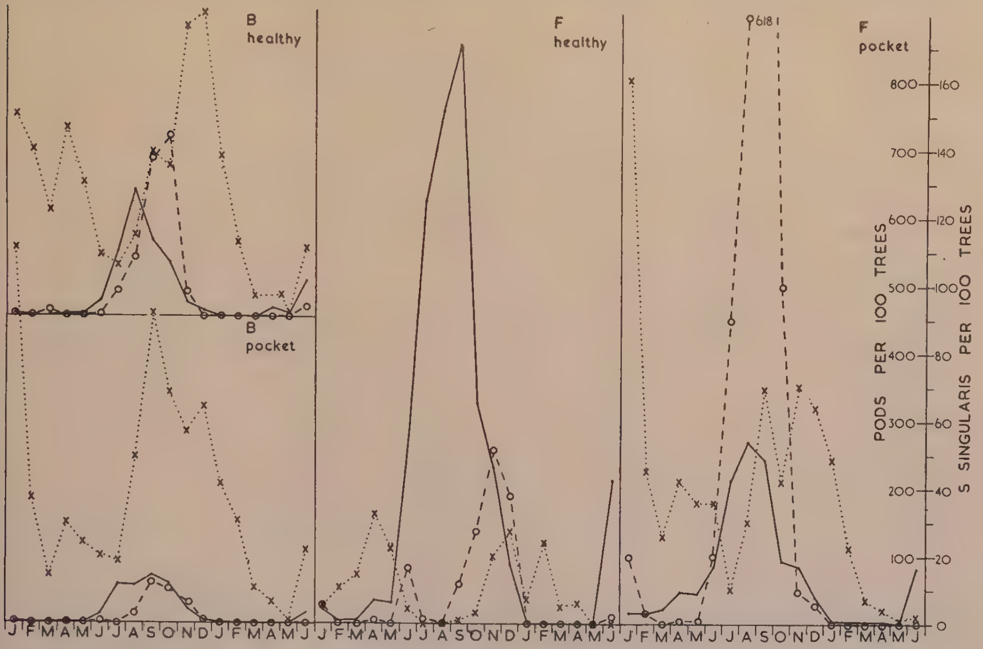


Fig. 2.—Fluctuations in the mean monthly population of *S. singularis* per 100 trees in four Observation Plots. (Symbols as fig. 1.)

A crucial experiment would be to remove all the developing pods from a large area and then measure the changes in population, but no body, either public or private, has consented to so drastic an experiment involving complete loss of crop. On a small scale, the experiment has been performed in stands of seedlings which are too young to produce fruit, and in advanced Mirid pockets where the yield has been totally suppressed. Counts in a plot of 288 seedlings were made by the observation plot method from April 1947, and the resulting estimate of the number of Mirids, including both *S. singularis* and *D. theobroma*, is given in Table I. *D. theobroma* is included in the count as it was the dominant species in the plot and it is only necessary to indicate here that the annual population change for this species is similar to that of *S. singularis* with the exception that the final stem maximum is often achieved about a month later. Even in the absence of pods, the Mirids increase at the same time of the year as in mature cacao.

TABLE I.

Mean number of Mirids per 100 trees per month in the seedling cacao Observation Plot.

	1947		1948			1947	
	S. singularis	*D. theobroma*	*S. singularis*	*D. theobroma*		*S. singularis*	*D. theobroma*
Jan.	+	+	10	47	July	0	10
Feb.	+	+	10	39	Aug.	2	12
Mar.	+	+	3	7	Sept.	3	10
Apr.	0	1	1	9	Oct.	15	15
May	0	10	0	8	Nov.	30	20
June	0	5	6	26	Dec.	7	11

+ No record.

In such a small plot, where no steps were taken to prevent migration from the surrounding cacao, it may be objected that the observed population change simply reflects a state of equilibrium with the Mirids in the adjacent bearing cacao but even where, as at Owena in Nigeria, cacao has been planted in a forest reserve at least a mile away from established cacao farms the same type of increase is seen (O. J. Voelcker, personal communication).

In the Daily Observation Plot, it was possible to estimate the part played by migration. Although the plot was in mature cacao the trees were so badly damaged that few pods were produced and the number of Mirids on pods was always negligible. The mean daily population of Mirids each month is given in Table II, and the figures show that the periods of high numbers coincide with those of bearing cacao. To estimate the extent of migration into the plot from the surrounding cacao, all adult Mirids known to have emerged from nymphs which had developed in the plot were marked on the pronotum with a spot of white paint. In this way it was possible to distinguish between the marked "endogenous adult" and the unmarked "exogenous adult" which had come into the plot after developing outside. The most likely source of error would be the failure to mark some of the truly endogenous adults if they flew from the tree on which they had developed before the observers came to mark them, and this would exaggerate the proportion of adults considered to be exogenous.

The aggregate time spent by marked and unmarked adults each month is shown in Table III. The first markings were made in the second half of November 1947, but the November counts have to be ignored to allow a period during which those adults, which had developed before marking began, could leave the plot. From December onward, the time spent in the plot by unmarked adults comprised only 30 per cent. of the time for *S. singularis* and only 38 per cent. of the time for *D. theobroma*, suggesting that the pocket was a focus of infestation for the surrounding cacao rather than a centre for colonisation. Interest centres on the months of December and January, for it is during this

TABLE II.

Mean daily population of Mirids per month in the Daily Observation Plot.

	1947		1948			1946		1947	
	S. singularis	*D. theobroma*	*S. singularis*	*D. theobroma*		*S. singularis*	*D. theobroma*	*S. singularis*	*D. theobroma*
Jan.	47	116	31	109	July	+	+	5	29
Feb.	22	124	13	106	Aug.	+	+	8	33
Mar.	20	36	7	30	Sept.	+	+	6	16
Apr.	6	21	3	32	Oct.	+	+	6	41
May	8	34	3	22	Nov.	+	+	28	51
June	10	49	3	14	Dec.	66	122	20	127

+ No record.

TABLE III.

The number of days spent in the Daily Observation Plot by marked and unmarked adults.

	S. singularis		*D. theobroma*	
	Marked	Unmarked	Marked	Unmarked
December 1947	32	22	39	34
January 1948	63	15	240	144
February	29	10	88	63
March	9	2	32	14
April	17	2	47	17
May	1	3	23	10
June	10	4	27	15
July	13	17	13	12
Total	174	75	509	309

period that adults from pods would be most numerous. Although the proportion of time spent in the plot by unmarked adults is higher than that for the complete sampling period, unmarked adults still contributed less than half the total adult time within the plot.

Adult/days have to be used rather than the number of adults because individual marks were not given to the endogenous adults, and the exogenous adults received no mark at all. Conclusions from the use of adult/days would be misleading if the time spent in the plot were different for the endogenous and the exogenous adults. This seems unlikely from marking experiments conducted prior to November 1947, when some adults developing within the plot were marked, the marking being timed so that only one marked individual of a given species and sex should be in the plot at one time. In this way it was possible to make observations on known individuals. Of the 35 individuals so distinguished 23 left the plot without visiting any further plot trees, *i.e.*, on leaving the tree upon which they had developed they moved straight out of the plot. A further ten left after making a visit to only one tree other than the one upon which they developed; one visited two trees; and one visited three trees. The endogenous adults, therefore, do not stay long in the plot and a comparable amount of random tree to tree movement was observed for unmarked adults. Furthermore, Williams (1953*b*) has shown that there is no difference between the time spent on a tree by an adult which had developed there and an adult which had arrived there by migration. It may be concluded that the difference between the number of adult/days spent by marked individuals and by unmarked individuals, during the second marking period, is not a result of a difference of behaviour between endogenous and exogenous adults, but is due to a difference in numbers of adults. This being so, the adults in the plot were preponderantly those that had developed there, and the balance of migration was outward rather than inward from the surrounding cacao. The normal cycle of population change was, therefore, a feature of the plot and not a reflection of equilibrium with the population in the surrounding cacao.

To summarise, there is an increase in the number of Mirids towards the end of the fruiting season but this increase is observed in all types of stand, whether bearing or not, and is a fundamental feature of Mirid populations. Pods are not the primary cause of such an increase, although their presence permits the build-up of a much larger population than would otherwise be experienced as they provide extra material upon which the Mirids can breed. Stems are provided fairly uniformly throughout the year, particularly by the damaged trees of Mirid pockets, so that food supply is not normally the limiting factor in Mirid multiplication. Food supply may be limiting only in the dry season when Mirid attack leads to the rapid wilting of chupons, under the prevalent conditions of low humidity, and new chupons are not proliferated.

A further distinctive feature of the annual cycle is the appearance of seasonal blast, a light but extensive killing of the terminal fans which shows as the typical damage of January and February. It has long been assumed that the increase in population beneath the canopy at this time is accompanied by a similar increase within the canopy and that it is this enhanced population which is responsible for the death of the twigs. None of the earlier sampling methods gave a picture of occurrences within the canopy: the Routine Collections were limited to hand-height and, although the whole of the tree was examined in the Observation Plots, the records distinguished only between fan and chupon. It was assumed that as fans were most numerous within the canopy and chupons below, this method of recording would clearly distinguish the canopy layer. In practice this was not so, as damaged trees produce chupons more uniformly along their total length than healthy trees, and these chupons jorquette to provide fans at all levels. Only for healthy plots does the fan category show the canopy layer, and in these plots there was no marked increase in Mirid numbers at a time to cause the observed seasonal blast. In the Mealybug Population Plots, the fans were mainly from the canopy, and the counts of lesions suggest that there was more feeding in the canopy during December and January than in the immediately preceding months; although the mean number of lesions per attacked fan remained fairly constant (5·1 in October, 4·9 in November, 4·8 in December, and 4·0 in January) the mean number of fans with lesions increased steadily from 43·1 in October to 65·6 in January. These conflicting results can be resolved in the single plot where the canopy was sampled separately from the sub-canopy and simultaneous counts were made of Mirid numbers and of lesions. As already indicated (Williams, 1953*b*), in this plot there was no increase in the *resident* canopy population at the time of increase in the lower layer. But, as can be seen from Table IV, there were more lesions on a common sample of 576 fans between November and February, the later-appearing lesions being responsible for seasonal blast. Seasonal blast is therefore a result of intensified Mirid feeding but does not imply that the *resident* canopy population is increased. At the end of the bearing season there is a very large population of Mirids in cacao and these, particularly the adult *S. singularis*, spread over the available feeding material, whether chupon or fan, whether within or beneath the canopy. But conditions are favourable for establishment only beneath the canopy and there numbers continue to increase: within the canopy the stems are subjected to more feeding, chiefly by adults, but fans do not provide suitable material for oviposition so that there is no increase in the number of established Mirids.

TABLE IV.

The number of Mirids and lesions within the canopy layer.

	Mirids	Lesions
August 1948	38	735
September	46	800
October	37	703
November	24	2084
December	31	1632
January 1949 ..	22	1502
February	12	1077
March	16	823

Mirid counts = total from 96 trees; lesion counts = total on 6 fans from each of 96 trees.

Maximum Population Levels.

So far, emphasis has been placed on the form of the annual population curve rather than upon the numbers of Mirids involved, but some estimate of the density to be anticipated at the time of population maximum would be useful. The Routine Collections would be expected to give an average figure for the Tafo area and the Observation Plots to give details of the distribution between good and bad cacao. The similarity between the maximum figures for *S. singularis* in the Collections, as in fig. 1, and the badly damaged cacao of the Daily Observation Plot, given in Table II, should then be attributable to differences between the intensity of attack in different years, and this is apparently confirmed by consideration of successive years in the Routine Collections. In fig. 3 are graphed the population changes of *S. singularis* for the last two years of sampling, and comparison with fig. 1 shows that the numbers involved were much smaller for this later period than for the earlier years. Fig. 4 is a comparison of the two periods for *D. theobroma* and similarly illustrates an apparent decrease with time. However, despite the smaller numbers involved it might be expected that the November/December increase on stems and seedlings should be shown in 1947, but this is not found in the Collections although it was true of the Observations Plots. This is explicable by a change in supervision at this time for. as described previously (Williams, 1953*b*), it had become clear, from the distribution of *S. singularis* and *D. theobroma* as determined by the Collections, that collections were not being made at random. Consequently, supervision was increased to ensure that strict randomisation was achieved and this change of technique was sufficient to lower the number of Mirids found. Without very close supervision, the collectors hurried past the healthy trees which would not yield Mirids and searched the more rewarding damaged areas. Further investigation showed that the sharp fall in numbers in 1946 also coincided with the arrival of a European entomologist who was detailed to look after the collectors for a short while. The main differences between years in the numbers of Mirids collected are, therefore, to be attributed to differences in the degree of supervision rather than to changes in Mirid numbers. That supervision should have such a marked effect may seem surprising but is substantiated by other results given later in this paper, for increased time with the collectors involved a corresponding lack of time with the Daily Observation Plot men who had previously been visited every day.

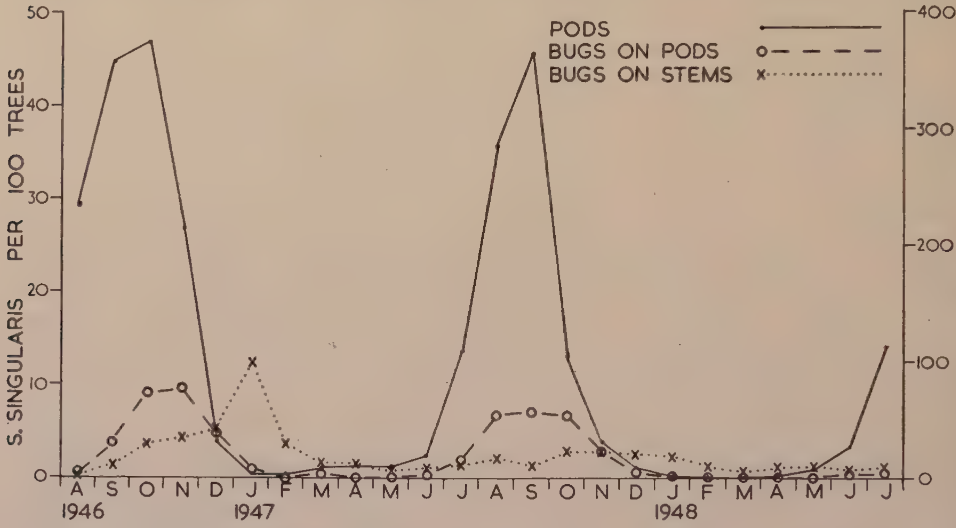


Fig. 3.—Fluctuations in the mean monthly population of *S. singularis* per 100 trees as estimated during the last two years of the Routine Collections. (For comparison with fig. 1.)

Counts made in the first two years of the Routine Collections approximate, therefore, to counts made in damaged cacao for the collectors went out with the determination to catch as many Mirids as possible and searched only damaged trees. Fortunately, such consistent application means that the form of the population curve is correct for as long as that system was maintained, and the same pattern is obtained if the numbers of Mirids are plotted against the mean day's effort per collector, a more appropriate unit than Mirids per 100 trees.

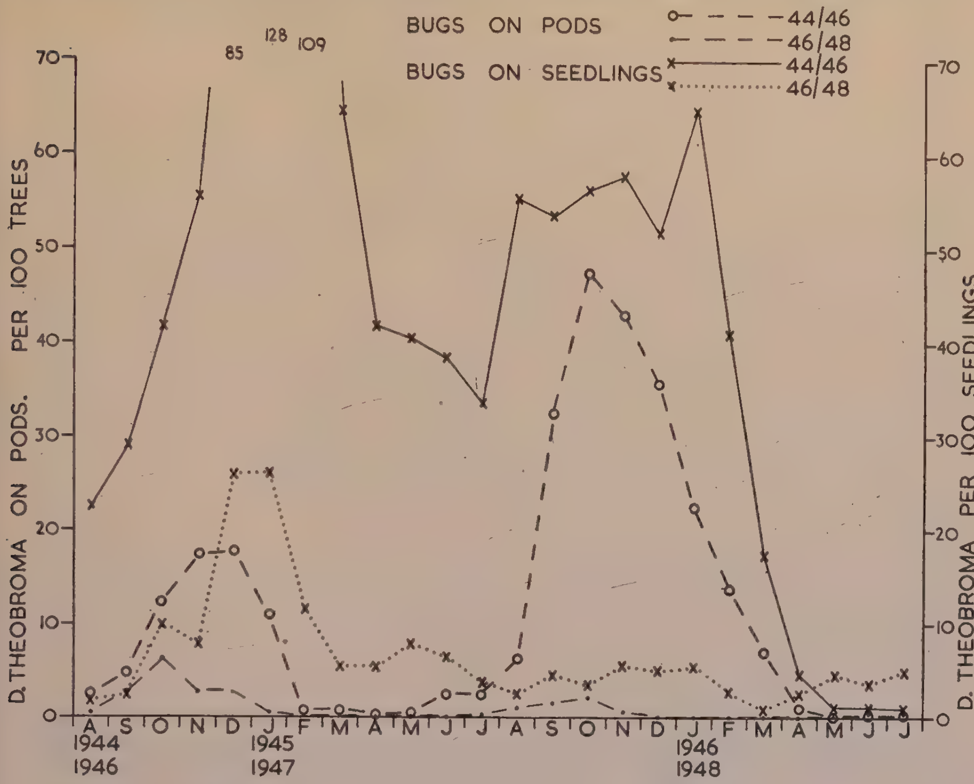


Fig. 4.—Comparison of the mean monthly populations of *D. theobroma* per 100 trees for the first two years and the last two years of the Routine Collections.

The collections suggest that the maximum numbers in damaged cacao should lie at about 200 Mirids per 100 trees and this estimate forms a useful check to the values obtained in the Observation Plots, which have the advantage of giving accurate counts, but the disadvantage of being too few to give reliable estimates for cacao in general. The observed maxima in the pockets sampled by the Observation Plot technique were as follows:

Frempong	72 (in December)
H_2	91 (in July)
H_1	142 (in January)
B	152 (in January)
F	215 (in January) and 697 (in July)
Daily Observation Plot	200 (in February)

These figures represent the total number of Mirids per 100 trees, including both species, those found on pods, and those on stems. Considering the wide differences between the plots, the dissimilarities are not great, suggesting a maximum of about 200 bugs per 100 trees.

The 697 Mirids recorded for plot F in July has been recorded separately in the above list for, in the writer's experience, it was quite exceptional, the pods swarming with nymphs and making counting very difficult. When trees are made especially suitable for Mirids, as by pollarding in the experimental initiation of Mirid pockets (Williams, 1953*a*), the initial population may far exceed the normal value of 200 per 100 trees as shown by the following means:

Plot	AC_2	304	Mirids per 100 trees
,,	P_3	440	,, ,, ,, ,,
,,	P_2	503	,, ,, ,, ,,
,,	AC_1	785	,, ,, ,, ,,
,,	P_1	1367	,, ,, ,, ,,

but this high density fell, in subsequent years, to the normal value of about 200 per 100 trees.

For comparison with other crop pests the best unit would be the number per acre, but 100 trees has been adopted as the unit because of the small size of badly infested areas. The average density of cacao trees in the Gold Coast is about 500 to the acre, giving the Mirid peak as 1,000/acre. This low number justifies the contention that the damage occasioned by Mirids is out of all proportion to the numbers involved. The contradiction between low numbers and the scale of damage is partly to be explained by the exaggeration of Mirid attack by exposure damage, as already emphasised (Williams, 1953*a*). The rôle of secondary effects becomes significant when it is remembered that the healthy trees of the plot designated F " Healthy " supported a peak incidence of 71 Mirids per 100 trees, a count virtually equal to that in the badly damaged plot named Frempong in the above list.

The estimate of 71 Mirids per 100 trees is high for healthy cacao in general so that it is particularly unfortunate that only one small plot of healthy trees was included in the Observation Plots. Cacao examined by the Routine Collections subsequent to November 1947 was mainly healthy and gave six Mirids per 100 trees as the peak population.

In seedling cacao, the individual plant, although smaller, may support as many bugs as a mature tree, and the greater plant density should allow a higher number of Mirids per acre. Again, the Observation Plots suffer from the drawback that only one seedling plot was sampled, and the infestation in this plot was noticeably low, giving a maximum count of 58 Mirids per 100 seedlings compared with 128 *D. theobroma* alone in the first year of the Routine Collections. To convert seedling infestations to numbers per acre is rather difficult as the native farmers' planting tends to be haphazard, but the seedling plot sampled at Adonkwanta (Williams, 1953*a*) had about 1,200 pickets to the acre which would give 696 Mirids per acre for the single seedling Observation Plot, and 1,500 *D. theobroma* per acre in the Routine Collections. Assuming that *D. theobroma* comprises half the total Mirids on seedlings, this would give a total of 3,000 Mirids per acre on seedling cacao.

Mortality.

A full acount of the life-history of the cacao Mirids, in all essentials the same for both species, has been given by Cotterell (1926) and may be briefly summarised as follows. The eggs are inserted beneath the bark of stems, or into the cortex of pods, leaving only a pair of slender filaments protruding, the magnitude and the relative lengths of the filaments being a reliable guide to the species of Mirid (Voelcker, 1949). There are five nymphal instars, the fifth moulting to give the winged adult, and the adult female remains incapable of oviposition for about a week. Estimates of the duration of each stage have been made with nymphs reared in the laboratory or caged in the field (Voelcker, 1949), but these are not wholly acceptable because of the artificial conditions. The measurement of the duration of each instar, under natural conditions, was possible in the Daily Observation Plot and the values obtained are summarised in Table V. These differ from the earlier estimates in that they show that the earlier instars are passed through more quickly than the later ones, whereas laboratory rearings suggested that all instars had approximately the same duration.

TABLE V.

Duration, in days, of nymphal instars under natural conditions in the Daily Observation Plot.

Instar	*S. singularis*		*D. theobroma*		Variance Period 1 / Variance Period 2
	Mean	Standard Error of Mean	Mean	Standard Error of Mean	
I ..	+	+	3·5	0·26	3·36
II ..	4·0	0·29	4·1	0·16	2·07
III ..	4·3	0·29	4·3	0·16	2·38
IV ..	4·5	0·34	4·4	0·18	2·19
V ..	5·8	0·56	5·4	0·31	1·37

+ Inadequate data.

It has been mentioned above, under the heading of population levels, that supervision of the Daily Observation Plot was relaxed from November 1947, a step which seemed justified at the time because of the high level of efficiency which observers had attained. The last column of Table V has been included to show the effect of relaxed supervision on the results, and has been obtained by dividing the variance (square of the standard deviation) of the period with daily surveillance by the variance of the period with relaxed surveillance. In examining the results derived during the second period it was noted that the figure, four days for instar duration, kept recurring with remarkable frequency, suggesting that the observers, noticing that the mean duration of a nymph was about four days, merely confirmed that the bug was present and derived the instar by calculation. The result was a marked drop in the variance as shown by the variance ratios in Table V. Consequently, in the computation of instar duration, only the results from the first period could be used, but the comparison of the two periods has been included here as it lends support to the theory that supervision has a marked effect upon the results obtained by the African field worker, and thus supports the contention that the differences between successive years of the Routine Collections were not real differences in the numbers of Mirids. Fortunately, the change from fifth instar to adult is so definite that it was recorded properly and calculations based on the total nymphal duration (Williams, 1953*b*) will not be affected.

The stage at which nymphs die can also be determined from the Daily Observation Plot if it is borne in mind that the observed loss during the last nymphal instar may be too high, as some may have changed into adults and flown away before the daily count began. Egg and adult mortalities are impossible to estimate in the plot, but to give an overall picture of the loss from a stock of Mirids these may be introduced from the laboratory findings. Adult mortality estimates are available from Tafo rearings. Egg mortality data at

TABLE VI.

Specific mortality ratios for successive stages in Mirid life-history, together with the estimated number of deaths and survivors from the mean egg number.

Stage	*S. singularis*				*D. theobroma*			
	Specific mortality ratio	Number at beginning of stage	Number dying	Number surviving to next stage	Specific mortality ratio	Number at beginning of stage	Number dying	Number surviving to next stage
Egg	†0·236	*51·2	12·1	39·1	†0·329	*32·3	10·6	21·7
Instar I ..	0·056	39·1	2·2	36·9	0·140	21·7	3·0	18·7
Instar II ..	0·179	36·9	6·6	30·3	0·229	18·7	4·3	14·4
Instar III ..	0·182	30·3	5·5	24·8	0·252	14·4	3·6	10·8
Instar IV ..	0·256	24·8	6·3	18·5	0·274	10·8	3·0	7·8
Instar V ..	0·424	18·5	7·8	10·7	0·465	7·8	3·6	4·2
Premature adult	*0·000	10·7	0·0	10·7	*0·000	4·2	0·0	4·2

†Data from laboratory rearings Owena.
*Data from laboratory rearings Tafo.

Tafo were completely unreliable so that, to complete the picture, recourse has to be made to rearings carried out at Owena, in Nigeria. The use of such diverse material can give only the general outlines of Mirid mortality but, as the detailed course of deaths for a natural population of insects has been examined for so few species, is none the less desirable as a first approximation.

The first column of Table VI gives the mortality at each stage of development, the value used being the specific mortality ratio calculated as follows:

$$\text{specific mortality ratio} = \frac{N^{o} - N_t}{N_o}$$

where N_o is the number at the beginning of each phase, and N_t the number which passes successfully to the next. So far as the pre-adult stages are concerned there is a gradual fall in the number of survivors. No nymphal instar is particularly subject to fatalities, the progressive increase in specific mortality ratio with later instars being due to the increased time spent in the older nymphal stages, so that if deaths are plotted against time rather than instar number the survivor curve is linear. Similarly, the high ratio for the egg stage is a result of an incubation period of a fortnight or so compared with a period of about four days for each nymphal instar. If reduced to unit time the mean loss per day during the egg stage is lower than that of the nymphs, doubtless due to the protected position of the egg, deep in the tissues of the host-plant.

If the estimates of mortality are at all realistic, calculation of survivors should give a single pair from a pair in the previous generation, or, as there is a steady mortality during the egg-laying period, the calculations should yield the same number of eggs as that assumed at the beginning. The laboratory rearings give a mean value of 51·2 eggs per female for *S. singularis* and column 2 of Table VI shows that applying the specific mortality ratios, 10·7 would survive to become mature adults. Assuming equality of sexes, 5·4 females would become mature. The Tafo rearings show that 3·4 eggs per female are laid per day of maturity and there is a daily loss of 1·1 females. On the first day of maturity, therefore, there will be 5·4 females and these will lay 18·4 eggs; on the second day, 4·3 females laying 14·6 eggs; on the third day, 3·2 females laying 10·9 eggs; on the fourth, 2·1 females laying 7·1 eggs; and on the fifth, 1·0 females laying 3·4 eggs. Thus the total number of eggs resulting from an initial number of 51·2 is 54·4, a remarkable agreement considering the widely divergent origins of the mortality data. For *D. theobroma* the fit is not so good. Starting with 32·3 eggs per mature female the number surviving to become mature adults is 4·2 (see Table VI). Of these 2·1 will be females, laying 2·7 eggs per day of maturity, the females dying at a rate of 1·1 per day. Thus, starting with a batch of 32·3 eggs the nett result is 8·4 eggs, suggesting that the mortality figures given are too high. The essential condition for equality in the number of eggs in successive generations is that the population is stable, neither increasing nor decreasing, and this holds for *S. singularis* in the Daily Observation Plot, despite violent fluctuations during the year. For *D. theobroma* the plot became less favourable and the mortality increased steadily toward the end of the sampling period. The specific mortality ratios quoted show that for this species, as for *S. singularis*, there is a steady fall in numbers during the nymphal period, and the fact that the nymphal values are all too high is a result of compiling the estimates from a contracting population. It becomes necessary, therefore, to relate the observed data to events within the Daily Observation Plot.

The relationship between population level and mortality is summarised in fig. 5 for *S. singularis* and fig. 6 for *D. theobroma*. The upper part of the graph represents recruitment into the population, the number of nymphs appearing in each month being plotted as blocks in the histogram, the total number of nymphs present for any part of the month being attained by adding, to the tops of the blocks, the number of nymphs surviving from the previous month. The continuous line represents the mean daily population of nymphs within the plot and this estimate follows closely the *total* number of nymphs present in any one month, though, owing to mortality, the scale of the mean daily population has to be exaggerated to effect coincidence with the histogram. In the lower section of each graph the histogram represents the number of nymphs which died before reaching the fifth instar in any one month. The full period, up to the emergence of the adult, is not used because of the uncertainty that disappearing fifth-instar

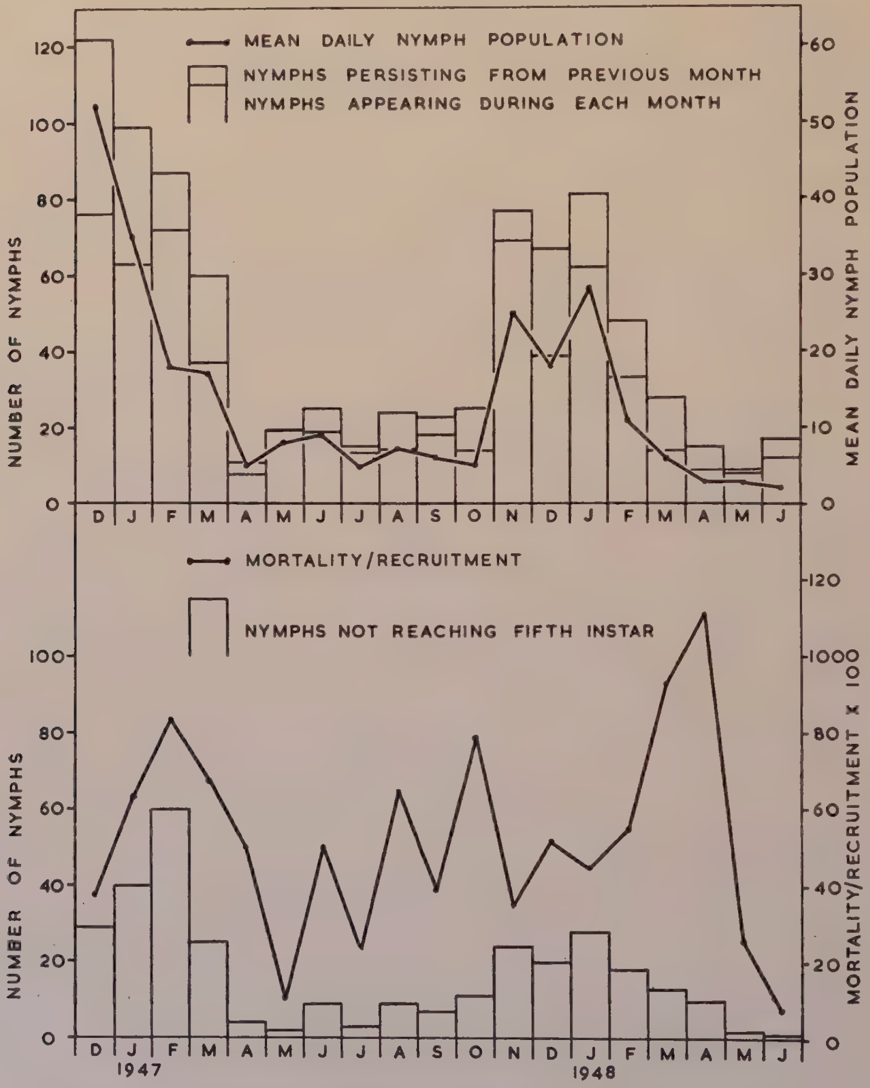


Fig. 5.—Recruitment and mortality of *S. singularis* in the Daily Observation Plot.

The upper graph shows the number of nymphs present during each month and the mean daily nymph population. The lower graph shows the number of nymphs which die before the fifth instar, and this number as a percentage of new hatchings.

nymphs have, in fact, died. The continuous line represents the nymphs dying before the fifth instar as a percentage of those appearing during the same month, *i.e.*, it is a representation of mortality, at a given time, as a fraction of recruitment. For both species the curves fall into three parts. Considering *S. singularis* first: from November 1947 to January 1948 there was an increase in the number of nymphs present and a corresponding increase in the mean daily population in the plot. Associated with these, the percentage mortality rose but the mortality curve lagged behind the population curve and reached its maximum in April, the relationship recalling the form of the prey-predator relationship demonstrated experimentally by Gause (1935). By analogy with this period, the first five months of the observations represent a similar pattern but

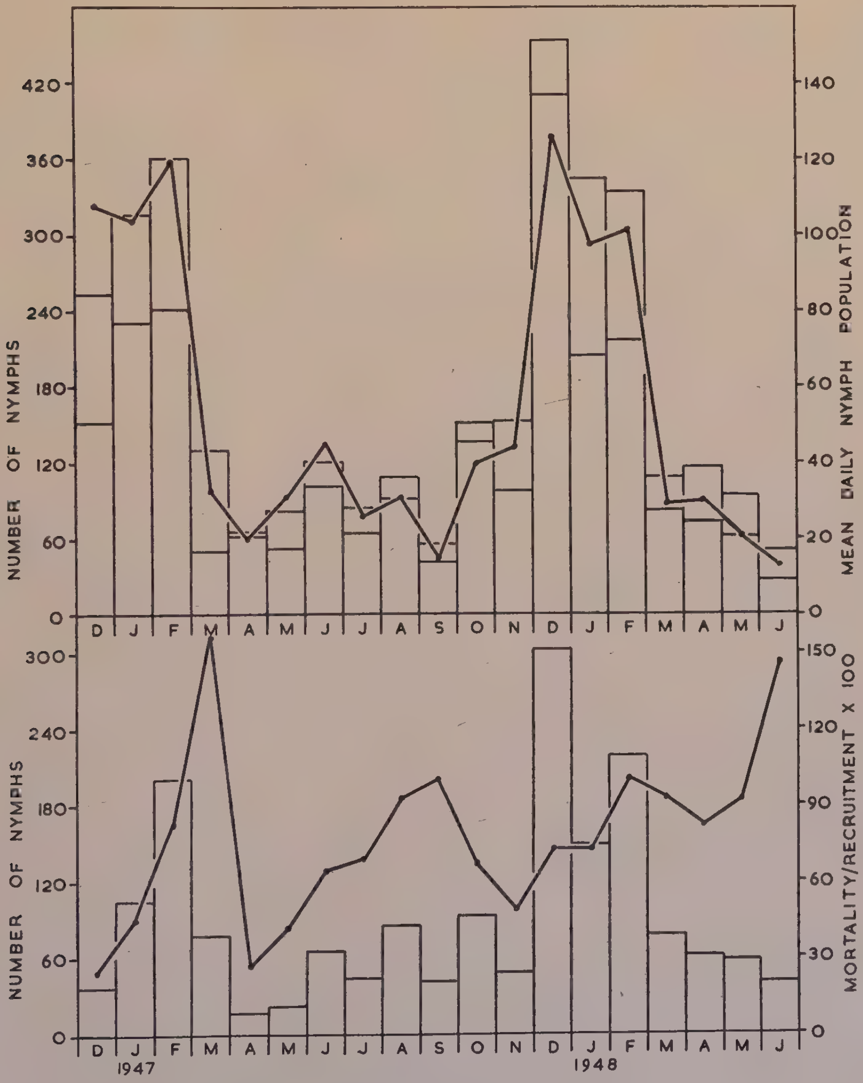


Fig. 6.—Recruitment and mortality of *D. theobroma* in the Daily Observation Plot. Symbols and legend as for figure 5.

the population increase corresponding to that in 1947 has not been sampled. The third part of the curve, between May and October 1947, was a period during which the mortality trend was upward, with fluctuations, but this upward trend was not related to population size, with the result that there was a slight, but definite, fall in numbers during this period. For *D. theobroma* the earlier periods were similar to those for *S. singularis*. December showed a high population which fell sharply as mortality increased to its maximum in April, and this was followed by a period during which mortality rose again and the population showed an irregular decline to a minimum in September. The last period began with the typical seasonal increase but became "irregular" in that, despite the fall in population from February, the percentage mortality did not drop to an anticipated minimum in April. Instead, after a slight drop, the mortality remained high, always more than 82·5 per cent. of the nymphs that appeared in any one month failing to reach even the fifth instar. This peculiarity is related to changes within the plot, for, toward the end of the sampling period the original trees were quickly dying out. Proliferation of chupons was very feeble and such chupons as were produced were quickly killed by the hatching nymphs, leading to the death of the nymphs themselves, with the result that mortality remained high. *S. singularis* was not affected to the same extent because of the smaller numbers, their more even distribution over the available food material and their ability to feed on stems, such as the woodier primary fans of the older chupons, not available to *D. theobroma*.

As no steps were taken to control Mirids, interest centres on the naturally operating controlling factors, particularly during the periods of peak population. The three main factors seemed to be the limited food supply, predation, and parasitism, all of which are density dependent. It must be admitted that parasitism is included as a guess. Nymphs were not collected for dissection to estimate parasite numbers and although the adult Braconid, *Euphorus sahlbergellae* Wilk. was seen active in the plot the number of such occurrences did not justify special records. Such information as we do possess of the levels of parasitism has been given already by Squire (1947) and by Voelcker (1945). It is of interest here to point out that, although parasitism of *S. singularis* may be as high as 30 per cent. of the nymphs, no parasite has been consistently found associated with *D. theobroma*. Squire (1947) recalls that Cotterell, on one occasion only, reared from *D. theobroma* the Encyrtid, *Encyrtus cotterelli* Wtstn., for which there is no subsequent record, and in a memorandum for internal circulation at W.A.C.R.I. there is a record by Box that a Euphorine parasite has been dissected from nymphs of *D. theobroma* "on a few occasions", a record which must be set against the very large numbers of nymphs dissected with negative results. This difference between two species of Mirid which show very similar annual population fluctuations raises several questions of fundamental importance which cannot be considered here as they have not been specifically investigated.

Again, the rôle of limited food supply can be described only in qualitative terms. Owing to the destructive nature of Mirid feeding, a small chupon is quickly killed when attacked by a number of nymphs and it has already been demonstrated (Williams, 1953*b*) that the period of nymphal development is prolonged at periods of high Mirid numbers, probably as a result of the deterioration of the attacked stems. This extension of life as an unwinged individual permits an increased toll to be taken by predators, but the dying chupon also causes a direct increase in death rate by reducing the food supply, particularly during the dry season when the tree does not respond by producing more stems to take its place. This is obvious in those instances where the death of the chupon is followed by the complete disappearance of the nymphs previously feeding on it. But, generally, it is difficult to know how much loss of nymphs is to be attributed to this factor for, from field observations, it is impossible to state when a stem has flagged to such an extent that it is no longer supplying adequate amounts of food, and there remains a fertile field for the experimental determination of the number of nymphs which can be supported by stems of various sizes and degrees of succulence, when parasites and predators have been excluded.

Mirid predators have been listed by Squire (1947). Two species of ant may be added to the list, *Pheidole megacephala* (F.) and *Camponotus* sp. F120 in the W.A.C.R.I. collection, which have been seen, in the Daily Observation Plot, actively consuming Mirid nymphs. In view of the number and variety of the possible predators, no estimation of their numbers was made in the Daily Observation Plot but, whenever a possible predator was seen on the same part of a tree as a Mirid nymph it was recorded. From such records it is possible to assess the action of general predators by noting the number of nymphs present before and after such a visit, and comparing this loss with losses where no predator was recorded. Mantids were the predators most frequently observed, with 160 records; ants came second with 98 records, though a small number of ant-mimicking spiders must be included in the 98 because the observers were unable to differentiate between the two; Reduviid bugs were the least frequent of the three with 39 records in association with Mirid nymphs. These appearances were followed by the loss of 184 nymphs, 83 following Mantids, 78 following ants and 23 following Reduviids. Taking a corresponding number of records, with the same time distribution but with no record of a possible predator, there was a loss of 33 nymphs, so that the circumstantial evidence suggests 151 nymphs were lost by predation. Applying the same correction factor to the individual instances it would appear that Mantids killed 16 per cent. of the nymphs with which they were associated, ants killed 21 per cent. and Reduviids killed 19 per cent., these overall levels suggesting that predators are a significant factor in the natural control of Mirid numbers. Moreover, death by predation follows the percentage mortality curves fairly well. For example, if the number of deaths which can be attributed to predation in any month is expressed as a percentage of the total number of nymphs present during the month, the values increase from 1 per cent. in December 1946 to 11 per cent. in March 1947, and from 2 per cent. in November 1947 to 20 per cent. in March 1948. Between these times the proportion fluctuated irregularly and, although no counts of predators were kept, the cause of changes in predator numbers (excluding ants) was fairly clear. Whenever the undergrowth within the plot grew sufficiently thick to impede the observers the whole plot was " brushed ", *i.e.*, these low plants were cut back. As the new undergrowth grew up, more, and more varied, niches were available for Mantids and Reduviids and the number of these in the plot increased, spreading on to the cacao trees. When due for brushing there were abundant predators in the plot and these disappeared quickly after brushing, to return when new growth appeared. The encouragement of undergrowth might seem to be a useful method of Mirid control but whenever the cacao canopy is broken, with resulting Mirid invasion, there is a natural increase in ground weeds and it simply remains to suggest that these should not be cut back, though it is doubtful if the Gold Coast farmer would do so except at harvest time.

None of the three types of general predator seems to be outstandingly more efficient than the others, yet the encouragement of ants, particularly *Macromischoides aculeatus* (Mayr) and *Oecophylla longinoda* (Latr.), has frequently been proposed as a possible control measure. This suggestion has arisen from the frequent observation that ants are found particularly on healthy trees, an association which is very striking when such trees stand isolated in severely damaged areas. A measure of this relationship is furnished by the Mealybug Population Plots, for the original records made by the mealybug workers included notes on the presence of ants together with estimates of the intensity of old Mirid damage on a scale where "damage absent" referred to trees with less than 1 per cent. of the twigs damaged, "damage slight" to trees with not more than 20 per cent. of the twigs damaged and "damage severe" with more than 20 per cent. damaged. Considering only the two species of ants most commonly suggested for Mirid control, Table VII shows the relationship between Mirid damage and the presence of ants for the trees felled from May to October 1947. Both species, and particularly *M. aculeatus* are associated with the healthier trees, the observed value of chi square being significant at the level P = 0·01.

TABLE VII.

Association between the ants, *Macromischoides aculeatus* and *Oecophylla longinoda*, and different degrees of old Mirid damage.

Species of ant present	Mirid damage			Total
	Absent	Slight	Severe	
M. aculeatus	12	61	10	83
O. longinoda ..	12	168	76	256
Neither	13	188	180	381
Total	37	417	266	720

chi square = 56·378.

Despite this relationship, Squire (1947) has opposed trials of ants as a control because the protection afforded to individual trees does not affect the well-being of their neighbours. This is well shown in the Daily Observation Plot where the following ant species were present:

Oecophylla longinoda (Latr.) on seven trees,
Macromischoides aculeatus (Mayr) on three trees,
Crematogaster (*Atopogyne*) *africana* Mayr on three trees,
Polyrachis (*Myrma*) *laboriosa* F. Smith on two trees,

with the following species, each on one tree,

Polyrachis (*Myrma*) sp. F.86 in the W.A.C.R.I. collection,
Camponotus sp. F.578 in the W.A.C.R.I. collection,
Camponotus sp. F.120 in the W.A.C.R.I. collection,
Pheidole sp. F.713 in the W.A.C.R.I. collection,
Crematogaster (*Atopogyne*) sp. F.141a in the W.A.C.R.I. collection,
Crematogaster (*Sphaerocrema*) sp. F.361 in the W.A.C.R.I. collection,
Crematogaster (*Sphaerocrema*) *striatula* Emery.

This list includes all the species of ants whose encouragement has been proposed for Mirid control, yet the attacked trees within the plot continue to deteriorate rapidly with no amelioration by their proximity to ant-bearing trees.

If fresh Mirid damage is taken as the measure of damage, the inadequacy of ants as controlling agents is even more striking, an inadequacy which is not surprising because ant numbers are not directly related to Mirid numbers. The Mirid workers in the Mealybug Population Plots estimated fresh damage by counting the number of new lesions, lesions which had blackened the attacked area of the stem but had not reached the canker stage. Table VIII gives the new relationship found. To make the results comparable with those for old damage a similar three-part scale was devised, "damage absent" including all the trees which were devoid of lesions, "damage slight" where the mean number of lesions per stem was less than ten and "damage severe" with an average of more than ten lesions per stem. These levels were adopted as being as nearly comparable to the earlier estimates as possible, but adjustment of the classes within wide limits makes very little difference to the significance of the results. For the counts covering the period of Mirid maxima, from September 1947 to February 1948, the value of chi square falls to 9·058, and does not reach significance at the level P = 0·05, suggesting an independent distribution of ants and fresh Mirid attack. That ants are most frequently found on healthy trees is due to the fact that trees which, for some reason, escape Mirid attack are the only ones suitable for colonisation, and the association is the reverse of control. *M. aculeatus* has never been observed to prey on Mirids, so that its suggested controlling efficiency was always a puzzle. There are records of predation by *O. longinoda* but at normal ant-population levels both the ant and Mirid nymphs

TABLE VIII.

Association between the ants, *Macromischoides aculeatus* and *Oecophylla longinoda*, and different degrees of fresh Mirid damage.

Species of ant present	Mirid damage			Total
	Absent	Slight	Severe	
M. aculeatus	25	46	2	73
O. longinoda	87	213	10	310
Neither	70	250	17	337
Total	182	509	29	720

chi square = 9·058.

TABLE IX.

Mean Mirid population per 100 trees per month in pollarded plot P_3.

	1947	1948		1946	1947
January ..	440	132	July ..	+	28
February ..	330	60	August ..	+	8
March	40	4	September ..	+	52
April	12	0	October ..	+	100
May	20	4	November ..	20	132
June	144	0	December ..	88	168

+ No record.

have been seen flourishing on the same tree. One observation of possible control by *O. longinoda* must be put on record. In Part I (Williams, 1953*a*), an account was given of an experiment to establish Mirid pockets by pollarding trees to induce chupon growth, and the subsequent history of two of the three plots was described. The third plot was not dealt with in that paper; the trees were pollarded on 16th September 1946 and chupons were present for the period of Mirid abundance so that large numbers were present in the plot, the mean number per 100 trees for the complete sampling time being given in Table IX. As the plot was better shaded than P_2, the trees did not succumb to Mirid attack but continued to support the bugs, which showed the seasonal increase again toward the end of 1947. At this time, the number of *O. longinoda* in the plot also began to increase and the virtual elimination of Mirids from the plot after February 1948 was almost certainly due to the action of the ants, although there is no adequate control plot to prove this contention conclusively. If this is an example of Mirid control by ants it is a method which can hardly be recommended, for the ant population was so high that it was an extremely painful experience to work in the plot and counts had to be made in short sallies, after which a retreat was needed to brush off the ants.

Discussion.

This survey of a number of field observations on the cacao Mirids has thrown some light on the factors determining the distribution of Mirid damage, on the relative distribution of the two species and the cycle of events in the annual population change. Perhaps sufficient information is available to direct insecticidal operations, for we know where the bugs are and when they are to be found, but, for any real understanding of the dynamics of Mirid populations, much more needs to be known. Where possible, the more obvious gaps have been indicated in the text, especially the need for experimental work, either on laboratory-reared individuals or on caged individuals in the field, to determine the effect of the more obvious physical factors on Mirid behaviour and bionomics. But it may not be amiss here to indicate some of the problems which need attention.

Despite a number of more or less inspired guesses, we do not know the loss in yield which results from Mirid attack and without such knowledge it will be impossible to evaluate the economics of control. Experimentally, information should be obtained by controlling Mirids in small plots, ignoring the cost, to find what increase in yield can result, thus giving the limits of return which may be expected from treatment and a guide to the cost which can be sustained economically. On a larger scale, the writer is convinced that the loss of crop experienced in the Gold Coast could quickly be estimated on the lines of the survey of cacao-growing areas already described, but with the rider that such a survey should be based on random choice and not under the restricted conditions which operated for the original survey. Both methods demand, as a first requisite, an exact definition of various intensities of damage, for there is a continuous gradation from slight attack with no obvious effect on the well-being of the tree to an advanced pocket with complete loss of crop. Such a definition is possible for mature trees by making use of the stages in the loss of cacao canopy which similarly varies from continuous and complete to total absence.

If such an evaluation of Mirid damage is made it should be carried out by one or a few entomologists familiar with all the phases of Mirid damage rather than by reports gathered from widely distributed sources. This is proposed because in the course of the Survey already undertaken it became clear to the writer that the term " blast ", for example, covers a multitude of symptoms in the general vocabulary of the Gold Coast. Much of the damaged cacao, especially in Ashanti and in Nigeria, which was confidently described to the writer as Mirid blast, whatever the cause of the damage, did not owe its condition to Mirid attack at all. It certainly shared with blast the death of the terminal twigs which continued to hang upon the tree when dry and brown but the dead twigs showed no sign of Mirid lesions.

If further field observations are contemplated, the sampling methods used should be much more critical than those which formed the basis of this series, for interpretation of the results has been continually hampered by the limitations of the sampling methods themselves. Sampling cacao Mirids is not easy because of the small number of bugs involved, coupled with the patchy distribution of damage and the contagious distribution of the bugs. It should be possible if the sampling unit were kept small, say ten trees, and strictly homogenous, in contrast to the plots used to date which were too large, and even when described as Mirid pockets included a ring of healthier trees around the periphery. Further, small sampling units would allow greater replication with its attendant advantages. Ladders prove very effective for badly damaged plots because there is no canopy to damage and the ladders may be as tall as the trees, but, despite great care, the use of 14-ft. ladders in better cacao causes disturbance and damage to the lower canopy branches. This could be overcome by erecting a permanent framework around the trees, with a removable catwalk allowing the observers to move about freely and search the canopy without damaging it. My opinion on the need for close supervision should be obvious from the text of this paper.

Summary.

For both of the important cacao Mirids, *Sahlbergella singularis* Hagl. and *Distantiella theobroma* (Dist.), there is a well-marked annual population cycle. Numbers are at their lowest in March and, although showing fluctuations from month to month, remain low until July. After this period, there is an increase in numbers to a peak level which may be bimodal, an earlier peak corresponding with the maximum numbers on pods and a later peak on stems alone in January or February. This is followed by an abrupt drop in the dry season to the minimum values of March.

The period of increasing numbers is, at first, associated with the presence of more cacao pods but evidence is given to prove that Mirid increase is not determined by pod increase but that both reflect the action of some common cause. The final peak population is associated with the symptoms of seasonal blast, but although Mirid numbers beneath the canopy are at their maximum at this time, there is no corresponding increase in the resident canopy population, the blast symptoms being produced by a transient population of adults from the sub-canopy levels.

Even at their highest the numbers of Mirids are small compared with most crop pests, the normal maximum being of the order of 1,000 per acre in mature stands of cacao.

Such aspects of mortality as could be studied from field observations are described. There is a steady loss during nymphal life, more dying during the later stages because these last longer. Parasitism, food supply and predation appear to be the main controlling factors, but, of these, only predation is examined quantitatively. Mantids, ants and Reduviids kill between 16 per cent. and 21 per cent. of the nymphs with which they are associated and the proportion of Mirids killed by such predators increases as the number of Mirids increases. Predation plays an important part in the natural control of Mirid populations but, although optimum conditions for predation exist in Mirid pockets, economic control is not effected.

The use of ants as a Mirid control measure is examined and rejected. Infestation of healthy trees by ants does not protect nearby attacked trees and the association between ants and healthy trees is due to the colonisation of such trees as the only ones suitable in an area subject to Mirid damage. A single instance is quoted where *Oecophylla longinoda* (Latr.) appeared to exert a control but only at a level where the ants were so numerous as to constitute a hazard to humans in the plot.

A final discussion of the three papers of the series is included to focus attention upon those aspects of Mirid biology which need immediate investigation. These include an evaluation of the loss caused by Mirids and the need for experimental work to determine the effect of physical factors on Mirids. Suggestions are made for sampling methods which could be employed in any future field observations.

Acknowledgements.

The field work which forms the basis of this paper was conducted while the writer was at the West African Cacao Research Institute. Thanks are due to those colleagues who gave assistance or advice, particularly to Mr. A. H. Strickland for identification of ants and for data from the Mealybug Population Plots. I am indebted to Professor A. Graham for permission to continue the analysis while in his department and to the Director of Cacao Research, W.A.C.R.I., for permission to publish this paper.

References.

Cotterell, G. S. (1926). Preliminary study of the life-history and habits of *Sahlbergella singularis* Hagl. and *Sahlbergella theobroma* Dist.—Bull. Dep. Agric. Gold Cst, no. 3, 26 pp.

Gause, G. F. (1935). Experimental demonstrations of Volterra's periodic oscillations in the numbers of animals.—J. exp. Biol., **12**, pp. 44–48.

Squire, F. A. (1947). On the economic importance of the Capsidae in the Guinean Region.—Rev. Ent., Rio de J., **18**, pp. 219–247.

Voelcker, O. J. (1945). West African Cacao Research Institute. Annual Report, April, 1944, to March, 1945.—36 pp.

Voelcker, O. J. (1949). West African Cacao Research Institute. Annual Report, April, 1947, to March, 1948.—85 pp.

Williams, G. (1953*a*). Field observations on the cacao Mirids, *Sahlbergella singularis* Hagl. and *Distantiella theobroma* (Dist.), in the Gold Coast. Part I. Mirid damage.—Bull. ent. Res., **44**, pp. 101–119.

Williams, G. (1953*b*). Field observations on the cacao Mirids, *Sahlbergella singularis* Hagl. and *Distantiella theobroma* (Dist.), in the Gold Coast. Part II. Geographical and habitat distribution.—Bull. ent. Res., **44**, pp. 427–437.

AIRCRAFT APPLICATIONS OF INSECTICIDES IN EAST AFRICA.

IX.—FURTHER EXPERIMENTS ON THE DEPOSITION IN OPEN COUNTRY OF A COARSE AEROSOL RELEASED FROM AN AIRCRAFT.

M H

By D. Yeo.

Colonial Insecticide Research Unit, Arusha, Tanganyika.

Previous papers (Yeo & Thompson, 1953, 1954) have described how atmospheric turbulence affects the rate at which a coarse aerosol, released from a low-flying aircraft, is deposited upon the ground in open country. The degree of atmospheric turbulence is measured by the factor

$$F = \frac{T_{10} - T_{2\cdot5} + \Gamma.\delta h}{(u_5)^2} \quad \ldots\ldots (1),$$

where T_{10} and $T_{2\cdot5}$ are respectively the air temperatures (in °F.) at heights of 10 m. and 2·5 m., u_5 is the mean wind speed (in f.p.s.) at a height of 5 m., and $\Gamma.\delta h$ is the numerical value of the dry adiabatic lapse over a height interval of 7·5 m. The cumulative ground deposit is calculated for various values of the ratio

$$t = \frac{\text{distance downwind in ft.}}{\text{mean wind speed in f.p.s.}} \quad \ldots\ldots (2),$$

which is a crude measure of the time interval between the production of the aerosol and the deposition of the droplets at a given sampling point.

In the previous work a constant aircraft height of 30 ft. was used, and it was shown that a high, positive, correlation exists between F, the measure of the degree of atmospheric turbulence, and the rate of deposition of the aerosol. Experiments have now been carried out with an aircraft height of 65 ft.; the results are not as complete as those for the lower height, but it is considered worthwhile to publish a short note on them, particularly since there will be no opportunity in the near future for continuing the investigation.

Experimental Methods.

The experimental techniques have been fully described elsewhere (Yeo & Thompson, 1954), so they are only briefly mentioned here.

A 10 per cent. w/v solution of technical DDT (80 per cent. p,p′ isomer) was used, with a solvent that consisted of equal parts by volume of Shell Power Kerosene and Shell Diesoline. The aerosol was produced by a boom-and-nozzle apparatus fitted to an Avro Anson aircraft. The apparatus has been described in detail in another paper (Hocking & others, 1954); for the experiments recorded in this note the boom was approximately 26 ft. long, and was fitted with 24 Bray "1" nozzles (cross-sectional area of orifice = 0·0128 sq. cm.) which pointed forward, directly into the slipstream. The emission rate was approximately 11 gallons per minute, and the aircraft speed was 110 m.p.h.

Ground deposits were measured colorimetrically, and for this purpose 0·75 per cent. w/v of the oil-soluble dye Waxoline Red was added to the basic solution. The drop spectrum was estimated by making counts upon glass plates, coated with magnesium oxide, which were placed upon the ground, and also from samples taken with cascade impactors (May, 1945). The mass median diameter was approximately 80 microns, and the diameters of the droplets varied from a few microns to approximately 200 microns.

Air temperatures were measured with clockwork-driven Assmann psychrometers, and wind speeds with Sheppard three-cup anemometers. Each experiment involved four runs by the aircraft and normally took 8–10 minutes to complete; during this period the average wind speeds were recorded, and average temperatures were obtained from frequent readings of the psychrometers. Aircraft heights were measured with a clinometer, and wind directions were obtained from the drift of smoke from a fire.

The values of F were calculated (equation (1)) for the same atmospheric layer as was considered in the work with the lower aircraft height. Time intervals were obtained by substituting into equation (2) the value of the mean wind speed at a height of 10 m., that is, mid-way between the ground and the aircraft.

The range of meteorological conditions was as follows:—

$T_{10} - T_{2\cdot5}$ varied from $+3\cdot6$°F. to $-1\cdot4$°F.
u_{10} varied from 4·2 f.p.s. to 14·7 f.p.s.

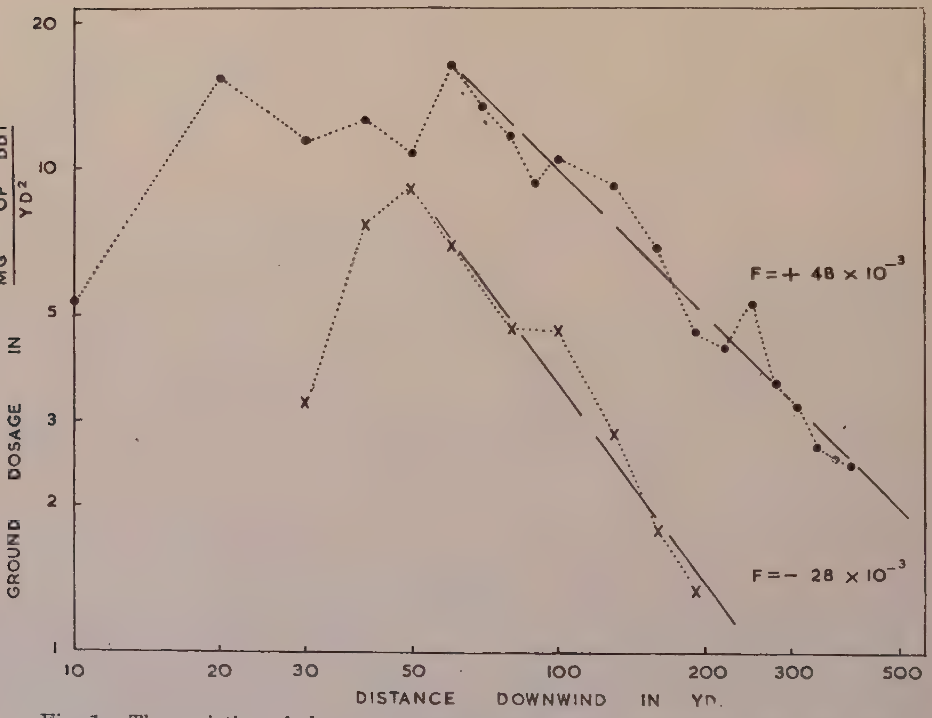


Fig. 1.—The variation of the ground dosage with distance downwind from the line of emission.

Results.

Two typical distributions of the ground deposit are shown in fig. 1, which illustrates the variation in ground dosage with distance downwind from the line of emission; the data are plotted on log-log paper. Deposits were expressed as proportions of the amount emitted from the aircraft, and were summed to various time intervals after production of the aerosol; fig. 2 shows how the amount deposited within 90 seconds is affected by the value of F, and it also includes similar results for an aircraft height of 30 ft. (Yeo & Thompson, 1954). The scatter of the points is large, but there is a high correlation between the amount deposited and F (correlation coefficient $r = 0{\cdot}77$, $P \ll 0{\cdot}001$). There is also a significant, but lower, correlation between the deposit and the temperature difference $T_{10} - T_{2\cdot5} + \Gamma.\delta h$ ($r = 0{\cdot}62$; $0{\cdot}001 < P < 0{\cdot}01$).

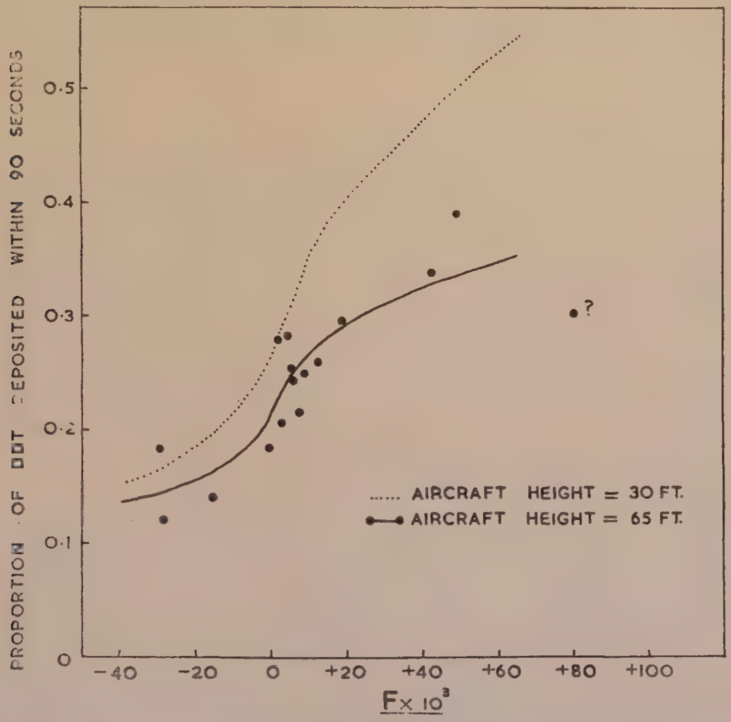


Fig. 2.—The dependence upon F of the amount of DDT deposited within 90 seconds.

The experiments were grouped according to their values of F, and average cumulative deposits were plotted against time interval. The results are shown in fig. 3, where the time interval is plotted on a logarithmic scale. For ease of comparison, similar groupings of data obtained with the lower aircraft height are included in the figure.

Discussion.

Increasing the aircraft height has had a not unexpected effect on the ground deposit. It may be seen from fig. 3 that the rate of deposition from 65 ft. is initially less than from 30 ft.; but for time intervals longer than 15–20 seconds it becomes greater, at least up to intervals of 90 seconds, which is the upper limit investigated in the work. For a given degree of atmospheric turbulence, fig. 3 suggests that, as the time interval increases, the total deposits from the two heights tend to approach the same value; this would have been expected from the nature of the physical factors affecting deposition.

The investigation has been empirical in that no attempt has been made to analyse mathematically the effect of the various factors upon the deposition.

The exact form of the deposit will depend greatly upon the drop spectrum of the aerosol, and more fundamental information will be obtained when an analysis is made of the deposition of droplets of various sizes; this is being done but it will take some time to complete.

Even in their present form the data are of considerable value. Combined with climatological surveys of atmospheric turbulence they allow a more realistic estimate to be made of the possibilities of using aircraft applications of coarse aerosols. They also help in the analysis of results; ground dosages can be deduced from relatively simple meteorological measurements and need not be measured directly.

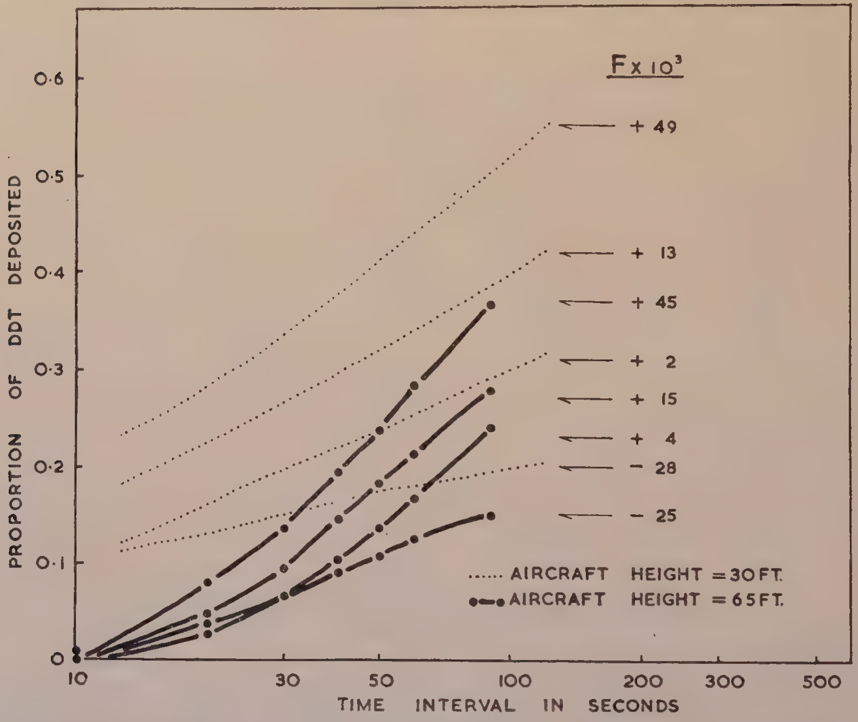


Fig. 3.—The variation with time interval of the total amount of DDT deposited upon the ground.

Summary.

Further experiments have been carried out to investigate how a coarse aerosol, released from a low-flying aircraft, is deposited upon the ground in open country. The aerosol had a mass median diameter of approximately 80 microns, and was produced by a boom-and-nozzle apparatus.

The aircraft height was 65 ft. It is shown that the rate of deposition is related to the degree of atmospheric turbulence, of which a simple and easily measured parameter is given. The rate of deposition is greatest when there is a large temperature inversion and a low wind speed.

A comparison is made with previous work where the aircraft height was 30 ft. Within the limits investigated, an increase in aircraft height reduces the deposits near the line of emission, but does not greatly affect the total amount that deposits within 150–200 seconds of production of the aerosol.

Acknowledgements.

The author is grateful to many members of the Colonial Insecticide Research Unit for their help; in particular to Mr. K. S. Hocking for much helpful discussion, to Dr. J. Robinson and Mr. E. T. Mesmer for carrying out the colorimetric estimations, and to Messrs. G. C. Dauber and H. H. Coutts for their assistance in the field work. The flying was very satisfactorily carried out by the staff of Messrs. Airwork Ltd.

The work has been directed by the Colonial Insecticides Committee, and was paid for from the Colonial Development and Welfare Fund.

References.

Hocking, K. S., Yeo, D. & Anstey, D. G. (1954). Bull. ent. Res., **45**, pp. 585–603.

May, K. R. (1945). J. sci. Instrum., **22**, p. 187.

Yeo, D. & Thompson, B. W. (1953). Nature, Lond., **172**, pp. 168–169.

Yeo, D. & Thompson, B. W. (1954). Bull. ent. Res., **45**, pp. 79–92.

A METHOD FOR ESTIMATING POPULATIONS AND COUNTING LARGE NUMBERS OF *APHIS FABAE* SCOP.

R

By C. J. Banks. 'E.H.N

Entomology Department, Rothamsted Experimental Station.

It is often necessary to estimate the numbers of Aphids in the field over a period of time, a problem which is accentuated when the species concerned is very numerous.

This paper describes a method for estimating population changes of the Black Bean Aphid, *Aphis fabae* Scop., on beans, and a simple volumetric method for counting large numbers of the Aphid in the laboratory. The method, which might be applied for other small arthropods, is illustrated by the results obtained from a study of three bean plots during the summer of 1952.

The essentials of the method are as follows: in the field, a large number of bean stems was examined and each placed in one of five arbitrary classes of Aphid infestation. Sample stems of each of these classes were removed from the plot to the laboratory and the Aphids on each stem counted. The mean numbers of Aphids for each of the classes, estimated from the sample results, were multiplied by the appropriate number of stems of each class and the products, when added, gave an estimate of the Aphid population of all the stems examined in the field.

The adoption of a system of classification of stems in the field not only allows a large number of stems to be examined but also eliminates the necessity of removing a large number of samples. Similar systems were used by Gorham in surveys of potato Aphids (see Broadbent, 1948) and by Ripper (1944) for Aphids on brussels sprouts. The present classification is developed from a method used by C. G. Johnson and J. A. Nelder (unpublished work) for Aphid populations of beans.

Selection of Samples.

Three plots were sown with beans of one variety during March 1952, each plot consisting of 12 rows, 35 ft. long and 30 in. apart. During May, estimates were made of the number of stems in each plot as follows:—Plot A: 2,088 (S.E. ± 62), Plot C: 2,988 (S.E. ± 79), Plot D: 2,604 (S.E. ± 56).

Primary migrants of *Aphis fabae* arrived on the beans during the week ended 21st May, and thereafter plots were examined once each week for the 8 or 9 weeks' duration of the Aphid infestations, Plot A on Tuesday, Plot C on Wednesday and Plot D on Thursday. On each plot, 13 to 14 per cent. of the stems were sampled by examining a fixed number of stems in each row; the total numbers of stems examined weekly on each plot were:—Plot A: 288, Plot C: 384, Plot D: 336.

Sampling was systematic in that the rows were always traversed in the same order and approximately every seventh stem was examined; but sampling was started from a stem chosen at random at the end of a row, and stems were selected at ground level to avoid bias in choosing stems infested by Aphids.

Classification of infested stems in the field.

Five arbitrary classes of Aphid infestation for the stems were adopted:

zero (O), where no Aphids could be seen;

very light (V), from one Aphid to a small colony confined to the very youngest leaves of the crown;

light (L), where there were several Aphid colonies present on the stem and not confined to the uppermost leaves;

medium (M), Aphids present in large numbers, not in recognisable colonies but diffuse and infesting a large proportion of the leaves and stem;

heavy (H), Aphids present in large numbers, very dense, infesting all the leaves and stem; the stem usually black with Aphids.

Occasional difficulty was experienced in deciding the appropriate class of an infested stem. The rule adopted, if one was in doubt, was to use the higher of two possible categories as it was believed that the tendency would be to underestimate rather than to overestimate the numbers. In practice, little difficulty was found in using this method and a short test, carried out to discover if there was any difference between two observers, showed no significant variation between the classification by each person.

The numbers of stems of the various classes for each plot for each week are given in Table I. From these it was possible to calculate the percentage of stems infested and to decide when the maximum infestation of a plot had been passed.

TABLE I.

Numbers of stems of the 5 classes of infestation on the bean plots A, C and D as classified in the field.

Class of stem	Plot A					Plot C					Plot D				
	O	V	L	M	H	O	V	L	M	H	O	V	L	M	H
Week 1 ..	221	67				243	138	3			153	183			
2 ..	181	103	4			203	166	14	1		108	221	7		
3 ..	166	110	11	1		168	177	29	8	2	80	184	61	10	1
4 ..	132	125	26	4	1	56	193	70	47	18	6	164	102	51	13
5 ..	55	129	74	29	1	4	113	102	117	48	0	1	38	186	111
6 ..	20	92	66	85	25	0	0	45	220	119	0	0	4	182	150
7 ..	0	49	78	105	56	1	0	15	208	160	4	18	98	190	26
8 ..	1	34	100	108	45	8	19	105	236	16	118	92	122	4	0
9 ..	28	75	142	43	0	241	93	45	5	0					

Numbers of stems examined each week were:— Plot A, 288; Plot C, 384; Plot D, 336.

Estimation of the Aphid Numbers of the Classes.

The average number of Aphids per stem in the various classes of the plots was then estimated, and it was necessary to know if there were significant differences between the classes of each plot.

Ten sample stems of each class were taken from each plot at various times during the course of the infestations. The samples were removed at a time when large numbers of a particular class were available and they were picked at random from all over the crop. Each sample stem was sealed in a container, taken to the laboratory and there washed individually in 90 per cent. alcohol in a large funnel. Aphids and their predators sank to the bottom of the spirit where they were run off through a tap; predators were removed at once and the Aphids stored in alcohol for counting at a later date.

Method of counting the Aphids.

There are several methods in use of counting Aphids, each with its advantages and disadvantages and with varying degrees of accuracy. Some workers have adopted the system of counting the numbers of colonies in the field, but although this method would be practicable for *Aphis fabae* on beans in the early stages of an infestation, it is of no use when the populations build up to the enormous numbers of insects at the height of the infestation. Ripper (1944) has employed a gravimetric method. C. G. Johnson (unpublished work) has used a system of withdrawing a fixed volume from a suspension of Aphids in water. Broadbent (1948) and Bradley (1952) have discussed methods employed in the field by various workers on potato Aphids. The present writer has developed the following volumetric method for *A. fabae*.

(1) The sample of Aphids from one stem was emptied into a dish and the alcohol drained off.

(2) With forceps and brush, a small quantity of Aphids was put into a small glass tube, 0·2 cc. capacity, into which some alcohol had been dropped to prevent the formation of an air bubble.

(3) More Aphids were added and packed in by gentle patting with a camel-hair brush until the tube was completely filled and the top level.

(4) The Aphids of the sub-sample were then emptied into a glass specimen tube with the aid of alcohol squirted from a plastic wash bottle.

(5) The operation was then repeated until the whole sample had been used up. This gave the total number of sub-samples, each in a separate specimen tube.

(6) The sub-samples were arranged in any order and six were selected at random.

(7) The six sub-samples were then counted accurately and the mean number of Aphids per sub-sample for that sample was calculated. This mean was then multiplied by the number of sub-samples to give an estimate of the total Aphid population of the sample. As an aid to counting, a modification of an apparatus described by Sims & Jordan (1941) was made; it consisted of an electro-magnetic counter operated by a microswitch from the A.C. main supply.

Example. Sample No. 32, Plot C (class H).

No. of sub-samples = 12 (+ 1 incomplete sub-sample).

6 random sub-samples contained Aphids as follows: 803, 791, 723, 748, 676, 769.

Mean Aphids per sub-sample = 752 (S.D. ± 47; S.E. ± 19).

Estimated number of Aphids in sample = 12 × 752 =	9,024
No. of Aphids in incomplete sub-sample =	520
Estimated total Aphids of sample	9,544

Samples classified as V or L had insufficient Aphids to allow six sub-samples to be taken. A proportion (about 25 per cent.) of all the sub-samples in class L was, therefore, counted and the mean number of Aphids per sub-sample for that class calculated. All class V samples were counted completely as were all the sub-samples of class L of Plot C.

The mean number of Aphids per sub-sample for all the classes of the three plots was 666 (S.D. ± 114); the means and standard deviations for the various classes are given in Table II.

To investigate the reliability of the method of sub-sampling, a test with three observers was carried out, using one sample. The sub-samples obtained by one observer were thoroughly mixed together for subsequent observers, so that each started with the complete sample. It was expected that the populations estimated by each person would vary considerably as the test proceeded, as the insects would become more and more squashed. Each person obtained a different mean number of Aphids per sub-sample (Table III) but the estimated total populations did not differ significantly from each other (P = 0·05) as indicated by the standard errors of the differences.

The average number of Aphids for each class of infested stem was next calculated. These means (Table IV) were estimated from the ten sample stems with accuracies of ± 24 per cent. (class V) and ± 16 per cent. (remaining classes).

TABLE II.

Mean number of Aphids per sub-sample for the classes of infested stem from Plots A, C and D.

Class of stem	Plot A		Plot C		Plot D	
	Mean	S.D. ±	Mean	S.D. ±	Mean	S.D. ±
L	657	116	686	143	699	95
M	650	88	732	100	779	253
H	509	63	674	83	611	85

Class V samples were counted completely.

TABLE III.

Estimates by three observers of the Aphid population of one sample bean stem (class H) from Plot A.

Observer	Mean Aphids per sub-sample ± S.D.	Number of sub-samples obtained	Estimated Aphid population of whole sample ± S.E.
C.J.B.	535 ± 30	36	19,260 ± 405
C.P.P.	647 ± 24	30	19,410 ± 252
L.R.T.	598 ± 41	33	19,734 ± 454

TABLE IV.

Mean number of Aphids per class of infested stem for the bean plots A, C and D, based on 10 sample stems of each class from each plot.

Class of stem	Plot A			Plot C			Plot D		
	Mean	S.D. ±	S.E. ±	Mean	S.D. ±	S.E. ±	Mean	S.D. ±	S.E. ±
V	100	86	27	97	66	21	190	144	45
L	984	336	169	1,769	780	247	1,511	1,129	357
M	5,205	2,205	697	7,660	2,699	854	9,736	4,056	1,283
H	12,833	3,843	1,216	13,010	4,917	1,556	19,413	6,027	1,907

The means of classes L, M and H for Plot D were significantly greater (P = 0·05) than those of Plot A, and in class H, greater than those of Plots A and C; in class L, the mean of Plot C was significantly greater than that of Plot A, while in class V none of the means was significantly different.

The Aphid populations of the 40 samples from Plot C, as estimated by this method, are plotted against the classes of infested stem in fig. 1 where the mean numbers of Aphids per class are indicated by crosses. Classes V, L and M appear to have been estimated in the field without difficulty; but there was no clear distinction between classes M and H.

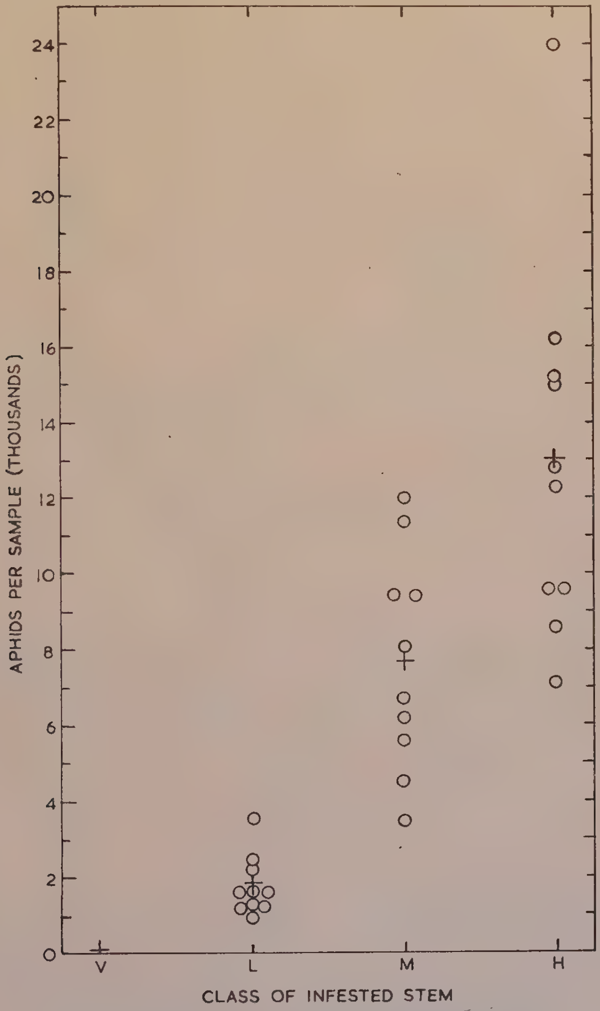


Fig. 1.—Populations of *A. fabae* on ten sample bean stems of each class of infested stem from Plot C.

Estimation of the Mean Number of Aphids per Stem for each Plot.

Estimates of the weekly total Aphid populations for the plots were obtained as follows: the numbers of stems in each class per plot per week, as obtained from the counts made in the field (Table I), were multiplied by the appropriate mean number of Aphids per class (Table IV); these, when added, gave for each plot a weekly estimate of the Aphid population, from which could be obtained the mean number of Aphids per stem for each plot (Table V).

TABLE V.

Estimates of the mean Aphids per stem for the plots A, C and D.

Week	Plot A		Plot C		Plot D	
	Mean	S.E. ±	Mean	S.E. ±	Mean	S.E. ±
1	20	17	45	22	93	22
2	46	29	125	40	150	93
3	90	36	403	71	720	250
4	248	69	1,917	428	2,778	745
5	863	264	4,458	1,048	11,974	3,004
6	2,907	742	8,628	2,173	13,958	3,474
7	4,676	1,107	9,639	2,517	7,459	2,364
8	4,311	1,039	5,738	1,685	717	415
9	1,288	423	331	99		

Summary.

A method for estimating population changes of *Aphis fabae* Scop. on bean plots is described. This involved the classification of bean stems in the field according to five arbitrary classes of infestation and the removal to the laboratory of ten samples of each class of infested stem for the estimation of their Aphid numbers. A simple volumetric method for counting large numbers of *A. fabae* is described and the results obtained from three bean plots are presented.

Acknowledgements.

The author is indebted to Dr. C. G. Johnson and Mr. J. A. Nelder for permission to mention their unpublished work. It is a pleasure to thank Mr. B. M. Church of the Statistics Department, Rothamsted, for advice on statistical matters, and Miss C. P. Pope for her assistance in field and laboratory.

The work formed part of a thesis for the Ph.D. degree, University of London, and was carried out during the tenure of a grant from the Agricultural Research Council to whom acknowledgement is made.

References.

Bradley, R. H. E. (1952). Methods of recording Aphid (Homoptera; Aphididae) populations on potatoes and the distribution of species on the plant.—Canad. Ent., **84**, pp. 93–102.

Broadbent, L. (1948). Methods of recording Aphid populations for use in research on potato virus diseases.—Ann. appl. Biol., **35**, pp. 551–566.

Ripper, W. E. (1944). Biological control as a supplement to chemical control of insect pests.—Nature, Lond., **153**, pp. 448–452.

Sims, A. L. & Jordan, R. C. (1941). A simple bacterial colony counting device.—J. sci. Instrum., **18**, p. 243.

PUPATION AND EMERGENCE IN *AËDES TAENIORHYNCHUS* (WIED.).

By E. T. Nielsen and J. S. Haeger. M A

Bureau of Entomology, Florida State Board of Health.

Ethological investigations of the salt-marsh mosquito, *Aëdes taeniorhynchus* (Wiedemann), have disclosed a rather special importance to the time of day of emergence. Interest has therefore focused on the happenings around this critical time in the insect's life. In order to understand emergence and the behaviour of the mosquitos immediately after emergence—including such important habits as mating and migrating—it was found necessary to have further information on some aspects of the development of the aquatic stages.

Field observations and rearing experiments were undertaken for this purpose at intervals between October 1951 and January 1953. It was hoped that a few experiments would be sufficient, but the problem was soon found to be considerably more complicated than expected, and the experiments reported here are only preliminary. From them, however, a few rather puzzling facts have been obtained, and an understanding of them may only be obtained by further experiments. Excellent conditions for such experiments will be provided in the proposed Entomological Research Centre of the Florida State Board of Health. The interruption occasioned by the establishing of this centre can be advantageously used in summarising the knowledge so far obtained.

Experimental Technique.

Since the technique varied from one experiment to the next, with some experiments being made in order to find the most suitable method, a short description of each experiment will follow.

Experiment 1.

About 30,000 fourth-instar larvae and a few pupae were transported in 60 half-pint ice cream cardboard cartons from the Big Pond in Fort Pierce the 75 miles to Archbold Biological Station, Lake Placid on 7 October 1951. They were placed in a room in which temperature and light could be regulated, the temperature at 28° to 30°C.* daytime and 19° to 22° night-time; "Sunrise" was simulated at 0730–0800 hr., and "Sunset" at 1945–2015 hr. As this experiment was made in order to get information on the behaviour of imagines of known age, only a few data on the larval development were recorded.

Experiment 2.

Larvae were obtained from a mangrove swamp on Sanibel Island (off the south-west coast of Florida), 20 November 1951. Emergence had been in progress several days. Most of the collection was of fourth-instar larvae, but there were also a few third-instar larvae and pupae. The natural water in the mangrove pools was rather dark and had a specific gravity of 1·005 at 22°.

The samples were taken to the laboratory at Lake Placid as fast as possible but many larvae died during transport. The remaining, healthy-looking larvae (all fourth-instar) were transferred to ice-cream cartons, 100 larvae to each. The surface area of a carton is 55 sq. cm., and the volume of water was kept at

---

* All temperatures in this paper are given in degrees Centigrade.

100 ml. by frequently adding distilled water which was kept in the room to avoid temperature shock. The experiment comprised five series:—

A. Natural water. No feeding until 0945 hr. on 24 November.
B. Natural water. Fed with dog biscuit once a day from 20 November.
C. As in B, but transferred to distilled water on 26 November.
D. At once transferred to distilled water; fed as B and C.
E. A single carton with 200 larvae in which the natural water remained unchanged and the dead larvae and exuviae were not removed. Fed as B, C, and D.

In series A there were 10 cartons, in B and C four cartons each, in D two cartons, and in E, as mentioned above, there was but one carton with 200 larvae. The cartons were placed on tables in the mosquito chamber. The temperature was kept at 27° to 28°; sunrise was simulated at 0900 hr. and sunset at 2100 hr.

Experiment 3 (29.xi. to 2.xii.1951).

Rain-produced, fourth-instar larvae and pupae were brought to the field laboratory on Sanibel Island from a natural breeding area on the island, 29 November 1951. They were kept in jars at room temperature (18° to 21°, mean 20°) and the emergence studied.

Experiment 4 (16 to 21.xii.1951).

A piece of sod from the Fort Pierce study area was flooded at the Archbold Station and the five emerging larvae kept in a one-gallon beaker. They were fed with standard food (pulverised dog biscuit + dry yeast, 1:1). Tungsten light 0730–2230 hr. plus ultraviolet light 1000–1030 hr.

Experiment 5 (14–29.ii.1952).

Rain-produced (2 to 3 February) fourth-instar larvae and a few pupae collected on Sanibel Island, 14 February 1952, and brought to the field laboratory for study of emergence. Kept at room temperature (17° to 23°, mean 20°). There were five series:—

A. 1,000 larvae were separated from the general collection at 1400 hr. on 14 February. On 17 to 21 February, 620 adults emerged but there was no pupation after 20 February. The remaining larvae were fed with pulverised dog biscuit and 60 more adults emerged between 25 and 29 February.
B. 109 individuals, pupated 14 February, 1400–1800 hr.
C. 219 individuals, pupated 15 February, 0000–0900 hr.
D. 178 individuals, pupated 15 February, 0000–2200 hr.
E. 136 individuals, pupated 15 February, 1000–2200 hr.

Experiment 6 (3 to 6.v.1952).

A batch of tide-produced larvae on Sanibel Island was brought to the field laboratory for observation. Pupation had just begun in the field. Kept under natural light conditions and at room temperature (mean 26°). Pupae were removed at hourly intervals and the resulting emergence recorded every hour.

Experiment 7 (3 to 10.xi.1952).

An egg-rich sod from Sanibel Island was flooded at the Archbold Biological Station. Half the larvae were kept singly in small glasses with 5 ml. water and fed with varying numbers of drops of standard food, 0·5 gm. ground dog biscuit plus 0·5 gm. dry yeast suspended in 50 ml. water. Temperature, 28°; light 1200–2300 hr. The other half of the larvae were kept, 5 together, in gallon beakers as in Experiment 4.

Experiment 8 (14 to 23.xi.1952).

Larvae were obtained as in the previous experiment and observations similarly made at the Archbold Station. Fed as in Experiment 7; temperature 28°. Seventeen series with different combinations of light, hatching time, and medium, the latter being distilled water (H), 2 per cent. NaCl solution (S), or natural water from a mangrove area (M) on Sanibel Island.

A. (AH, AS, AM) in daylight, hatched 14 November at 0000 hr.
B. (BM) ,, ,, ,, ,, ,, ,, 0800 ,,
C. (CM) ,, ,, ,, ,, ,, ,, 1600 ,,
D. (DH, DS, DM) artificial light 2300–0900 hr. hatched 14 November at 0000 hr.
E. (EH, ES, EM) ,, ,, ,, ,, ,, ,, ,, ,, ,, 0800 ,,
F. (FH, FS, FM) ,, ,, ,, ,, ,, ,, ,, ,, ,, 1600 ,,
G. (GH, GS, GM) in darkness, inspected and handled by weak dark red light. Hatched 14 November at 0000 hr.

Experiment 9 (1 to 8.xii.1952).

An egg-laden sod from Sanibel Island was flooded with tapwater in pans at Archbold Station and the sod removed after about 36 hours. Fed with standard food as in Experiment 7; temperature 29°. Four series, with varied hatching and light times:—

A. Flooded 1 December at 0000 hr. Light 2200 hr. "midnight" 1600 hr.
B. ,, ,, ,, ,, 0800 ,, ,, ,, ,, ,, ,, ,,
C. ,, ,, ,, ,, 1600 ,, ,, ,, ,, ,, ,, ,,
D. ,, ,, ,, ,, 0000 ,, Constant darkness.

Experiment 10 (21 to 29.i.1953).

The same type of sod as in the preceding experiments was used but most of the eggs, now 5 or 6 months old, seemed to be dead. Of six series started, only two successfully produced larvae:—

A. Flooded 21 January at 0930 hr. Larvae poured off at 1120 hr. Kept in constant light.
B. As in A but a lid was placed over the pan every day between 2000 and 1000 hr.

Duration of Larval Stage.

Effect of temperature.

The duration of the larval stage is dependent on several factors. Water temperature is indisputably important and under natural breeding conditions is probably the main factor. During the summer months in Florida, when the mean temperature is about 30°, the interval from hatching to pupation is not usually more than five or six days. A frequent situation is for the first three instars to last one day each and the fourth instar 2 to 3 days, or a little less than the first three instars put together. In the colder seasons, larval development may last 2 to 3 weeks.

Recent observations made under actual field conditions on Sanibel Island in late July and early August showed that the larval period could be as short as 3 to 4 days. This occurred in water exposed to direct sunlight and not over 1 to 3 inches deep, where the temperature ranged between 27° and 38° throughout the day. These pools were in a grassy, mowed-over field; the larvae could not escape the warm water. The same rainfall had hatched eggs in many depressions on the island. In one large swale, where the water averaged 10 to 12 inches in depth, with many large areas 18 inches deep, and where there was plenty of shade, it was observed that it took 6 to 7 days for 5 per cent. and 9 days for about 10 per cent. of the larvae to reach pupation. In the shallow pools mentioned earlier there was little difference in temperature between top and bottom, but in this larger and deeper swale, water temperatures averaged 33° at the surface and 28° to 29° six to twelve inches below the surface. It was noted that the larvae spent most of their time at these cooler depths.

Unfortunately, all the experiments in which the larvae were hatched from eggs in the laboratory were made at 28° or 29°. There are therefore no experimental data on the influence of temperature on the larval development.

Effect of other factors.

Even at uniform temperature, however, there is a considerable variation in the duration of the larval stage. Table I gives the data for all the experiments in which the age of the larvae was known. It will be seen that in the experiments with few individuals the duration of the larval stage is shorter than in the " big " experiments, nos. 8 and 9. In Experiment 8, about 7 larvae remained, unpupated, after the ninth day while in Experiment 9 the pupation by the ninth day represented less than half the larvae. In the earlier experiments, in which the age of the larvae was unknown, there had been experienced the same phenomenon of prolonged larval stage, usually combined with very high mortality.

TABLE I.

Age of pupation for all experiments in which hatching time was known.

Experiment number Number of pupae	4 5	7A 11	7B 4	8 403	9 770	10 18
% pupated on:—						
5th day (96–119 hr. old) ..	100		75	13	12	50
6th day (120–143 hr. old) ..		91	25	49	24	44
7th day (144–167 hr. old) ..				34	12	6
8th day (168–191 hr. old) ..		9		4	46	
9th day (192–215 hr. old) ..					6	
Mean age (in hours) at pupation ..	98	133	121	141	158	138

Only pupation previous to 10th day is considered in this Table. Temperature (28°–29°C.) and feeding conditions uniform for all experiments.

That the factor involved is hunger was demonstrated in Experiments 2 and 5. In Experiment 2, fourth-instar larvae were brought in from the field; 1,000 larvae were fed with dog biscuit every day and yielded 442 pupae, another batch of 1,000 larvae were not fed for the first 88 hours, by which time only 6 per cent. had pupated. In the larval group which had been fed, pupation went on, but no pupae appeared among the unfed larvae during the next four days. Pupation was resumed only 60 hours after these starved animals were fed, but the total number of pupae from this batch of 1,000 larvae was only 223. In the fifth experiment the same thing occurred. In series A, containing 1,000 fourth-instar larvae, pupation stopped after 3 to 4 days of hunger. The remaining larvae pupated only after feeding was started.

The delay in development and high mortality in Experiment 9 were probably also caused by insufficient food intake. In that case, however, it was not because there was too little food present but because too many animals were kept together in large pans with but little water. Most of the feeding takes place at the bottom, and it was observed that the feeding larvae were incessantly disturbed by those wriggling to the surface for respiration. Under crowded conditions it might be dangerous for larvae in a feeding stage if the depth of water is less than 3 to 4 cm. At the other extreme, living completely isolated seems also to delay development. In Experiment 7, half of the individuals (7B) were kept, five together, in gallon beakers (as in Experiment 4); 5 pupated on the fifth day and 3 on the following day, all of them when 115 to 124 hours old. Among the nine larvae isolated in small vials (7A) the first pupated at 139 hours and the last when 189 hours old.

The larvae probably feed mostly during the first half of each instar. In the case of fourth-instar larvae introduced into waters containing radioactive phosphorus for marking, it was observed that the increase in larval radioactivity took place mostly in the early part of the stage (Dr. Maurice W. Provost, personal communication).

In Experiment 8 an attempt was made to evaluate the rôle of water characteristics in setting the duration of the larval stage. Table II gives the results.

TABLE II.

Age at pupation in different types of water.

Type of water	Distilled water	2% NaCl	Mangrove water
Number of pupae	191	117	95
% pupated on:—			
5th day (96–119 hr. old) ..	12	12	15
6th day (120–143 hr. old) ..	47	42	59
7th day (144–167 hr. old) ..	34	44	25
8th day (168–192 hr. old) ..	7	2	1
Mean age (in hours) at pupation ..	141	139	132

Data from Experiment 8.

The fastest development occurred in the mangrove water but the differences were too small to warrant a definite conclusion. No important error, if any, was made in pooling the results of the three series.

Sex differences.

From the earliest experiments it was evident that those larvae which later became male adults pupated before those which became female imagines. In all experiments it was found that the first pupae isolated in a brood became mostly males while the last ones became females. From the experiments in which the time of hatching was known and in which the pupae were isolated, it is possible to give figures for the duration of the development of the two sexes. It is seen in Table III that the larvae of females were considerably slower in developing than those of males. Before discussing these findings any further, another peculiarity of pupation must be considered.

The 24-hour rhythm in pupation.

It was evident from the earliest experiment that emergence of imagines was not evenly distributed over the 24 hours but had a definite daily maximum; this will be discussed below. In the second experiment the same was found to be

TABLE III.

Sexual differences in the duration of the larval stage.

Sex Number of individuals	Male 90	Female 89
% pupated on:—		
5th day (96–119 hr. old) ..	23	6
6th day (120–143 hr. old) ..	64	36
7th day (144–167 hr. old) ..	13	57
8th day (168–192 hr. old) ..		1
Mean age (in hours) at pupation ..	129	145

Data from Experiments 4, 7, 8D, 8E, 8F, and 10.

TABLE IV.

Distribution by percentage of pupation over 24 hours in all experiments with dark and light periods.

Experiment	2	4	6	7	8A–F	9A–C	10	Mean
Number of animals	754	5	1,886	15	315	432	18	3,424
Hour of pupation:—								
00–03	7	0	0	0	4	9	0	3·2
03–06	4	0	0	0	1	1	0	1·1
06–09	5	0	0	0	3	0	6	1·5
09–12	8	0	0	0	9	2	0	2·8
12–15	17	0	1	40	27	11	11	8·4
15–18	34	0	11	47	27	9	17	17·7
18–21	17	80	67	13	22	43	44	48·2
21–24	8	20	21	0	7	25	22	17·1

Time is given as hours (00 to 24) beyond experimental midnight (00 hour) which is the midpoint of the period of darkness, whether natural or artificial.

TABLE V.

Distribution by percentage of pupation in relation to different 24-hour datum types.

	Alternating light and darkness			All darkness
	1	2	3	4
Hour made 00 below	Exp. midnight (as in Table IV)	Midnight E.S.T.	Hatching hour	Midnight E.S.T.
00 – 03	3	8	12	12
03 – 06	1	7	16	3
06 – 09	2	7	8	23
09 – 12	3	15	16	17
12 – 15	8	10	12	6
15 – 18	18	11	10	7
18 – 21	48	19	12	16
21 – 24	17	23	14	16

Based on same data as Table IV, plus Experiments 8G and 9D (column 4).

the case with pupation, and this has been confirmed by all the experiments recorded in Table IV. Briefly stated, it is seen that 83 per cent. of all pupation took place during the evening periods (15 to 24 hours after experimental midnight) and 48 per cent. in the period just after sunset (18 to 21 hours after experimental midnight). That this period of maximum pupation is determined by the distribution of light and darkness is beyond doubt, as the following will attest.

The pupation times in Table IV are arranged according to hours (00 to 24) beyond experimental midnight, which is the midpoint of the period of darkness, whether natural or artificial. Arranged according to "civil time", *i.e.*, Eastern Standard Time (Table V, col. 2) the daily maximum nearly disappears; if arranged according to hatching time (Table V, col. 3) the maximum disappears. Neither is a daily rhythm of pupation discernible in the case of larvae reared in darkness (Table V, col. 4). It is obvious then that the 24-hour pupation rhythm occurs in the mean only when the experiments are pooled according to the actual change of light and darkness. The maximum occurs around sunset.

With this knowledge it might be worth while to examine the hour of hatching of the eggs in relation to experimental midnight. In Experiments 8 and 9 hatching was effected at 8-hour intervals with this point in view. Unsuitable technique delayed larval development in the ninth experiment, so Table VI presents the data from Experiment 8 only. Differences attributable to hatching hour were very slight, which can only mean that the tendency to pupate around sunset has just as much accelerating as retarding effect on the larval development.

TABLE VI.

Duration of the larval stage in relation to the hour of hatching.

Experiment 8, Series:—	A + F	B + D	C + E
Number of individuals	187	55	73
Hatching hour	00 hr.	08 hr.	16 hr.
% pupated on:—			
5th day (96–119 hr. old) ..	16	7	10
6th day (120–143 hr. old) ..	43	53	63
7th day (144–167 hr. old) ..	34	40	27
8th day (168–192 hr. old) ..	7		
Mean age (in hours) at pupation ..	140	140	136

Data from Experiment 8.

The Pupal Stage and Emergence.

Influence of temperature.

Of the three factors found to affect the rate of larval development, one may at once be excluded—nutrition—since the pupae do not eat.

Concerning the effect of temperature, the experiments here considered gave a somewhat better knowledge in the case of pupae than of larvae. In series B of the fifth experiment, pupal development took place at a rather constant temperature of 20·8°, while in Experiment 6 the temperature had a mean of 25·5°. In Experiments 4 and 7 to 10 the mean temperature was fairly constant at about 29°. The duration of the pupal stage in these experiments, as reflecting the temperature effect on rate of development, is summarised in Table VII. Fig. 1 shows that the reciprocal of the duration is a straight-lined function of the temperature. Taking the crudeness of the experiments into account, the approximation is surprisingly good. As the only factor at variance in these groups of experiments was the temperature, it seems justified to consider temperature as the only environmental factor of importance in establishing the duration of the pupal stage.

TABLE VII.

Duration of pupal stage in relation to temperature.

Experiment	5B	6	4, 7–10
Number of individuals . .	109	1,716	450
Temperature (°C.) . .	20·8	25·5	29·0
Pupal duration (in hr.)			
male	61·9	44·7	36·7
female	60·0	45·7	37·5

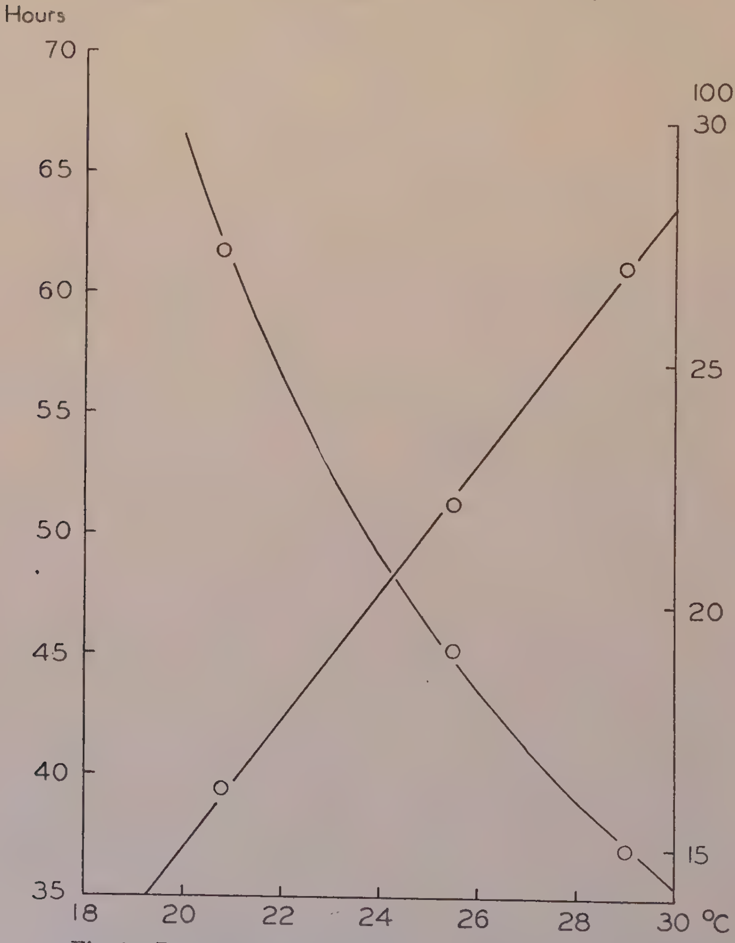


Fig. 1.—Duration of the pupal stage and the velocity of the pupal development in relation to temperature in *Aëdes taeniorhynchus*.

The 24-hour rhythm in emergence.

In all the experiments without any exception, and in all observed cases in nature, it has been found that the emergence is not evenly distributed over the 24-hour period but has rather a marked maximum at a certain time of the day, as was found also to be the case with pupation. There is, however, one important difference; maximum pupation was always found to be around the change from light to darkness, but maximum emergence might take place at any time of the day. The reason for this is of course easily understood. If the maximum of pupation, as the effect of the day-night rhythm, is fixed to the period of sunset and the duration of the pupal stage is influenced solely by temperature, it follows that there must be a maximum of emergence which will be at the same time every day during the emergence of the same brood but which may be at any hour of the day, depending on temperatures. "Brood" in the sense just used means a group of animals resulting from a simultaneous hatch and developing at the same temperatures. In experiments with different temperatures and in different breeding areas or seasons in the field, the resulting maximum of emergence will occur at different times of the day.

As will be seen from Table VIII all experiments with daily changes from light to darkness and with the temperature at 29° gave a maximum emergence in the morning, corresponding to the 37-hour duration of the pupal stage superimposed on sunset time pupation. In Experiment 5B the emergence maximum was also in the morning, corresponding to the pupal duration of 62 hours, very close to 24 hours more than at 29°. And in Experiment 6, maximum emergence occurred at the same time of day (sunset) as the maximum pupation; the duration of the pupal stage at 25·5° was 45 hours or almost two days. And finally, the last column of Table VIII shows that when the animals developed in darkness there was no daily maximum of emergence.

TABLE VIII.

Distribution by percentage of the emergence over the 24 hours, experimental midnight (00 hr.) being the midpoint of the period of darkness whether natural or artificial, or civil (E.S.T.) midnight in the case of continuous darkness.

	Alternating light and darkness			All darkness
Experiment	5B	6	4, 7, 8A–F, 9A–C, 10	8G, 9D
Number of individuals	109	1,716	564	133
Temperature (°C.)	20·8	25·5	29	29
Exp. hour of emergence				
00 – 03	7·4	0·2	9·4	20·1
03 – 06	22·0		22·0	10·8
06 – 09	49·5		32·7	12·9
09 – 12	17·4		23·1	8·2
12 – 15		0·8	1·9	4·9
15 – 18		9·1	7·4	16·4
18 – 21	2·8	68·7	0·8	11·0
21 – 24	0·9	21·7	2·7	15·7

Sexual difference in emergence.

In the preceding remarks no attention has been paid to the difference between males and females in pupal duration because this difference is very small, 0 to 2 hours. But, as shown above, there is a rather marked difference in the larval duration which is carried over to the emergence. For the group of experiments given in Table III the mean age at pupation was found to be 129 hours for males and 145 for females. The mean age for the emergence of the same 179 animals was 166 hours (males) and 182 hours (females) so that the sexual difference in both larval and pupal duration is 16 hours.

As mentioned above, emergence takes place over several days with a maximum each day at the same time. The sexual differences in development will therefore cause a preponderance of males during the first emergence maxima and of females in the last. The largest homogenous material including complete brood histories available from the experiments are the pooled experiments 8A and 8F. They give a very typical picture (fig. 2). The emergence lasted five days, of which the first had a small maximum consisting solely of males. On the second day there emerged the largest number of males, and a few females. The third day, nearly the same number of each sex emerged. The fourth day more females than males emerged. And finally on the last day a few females and no males emerged.

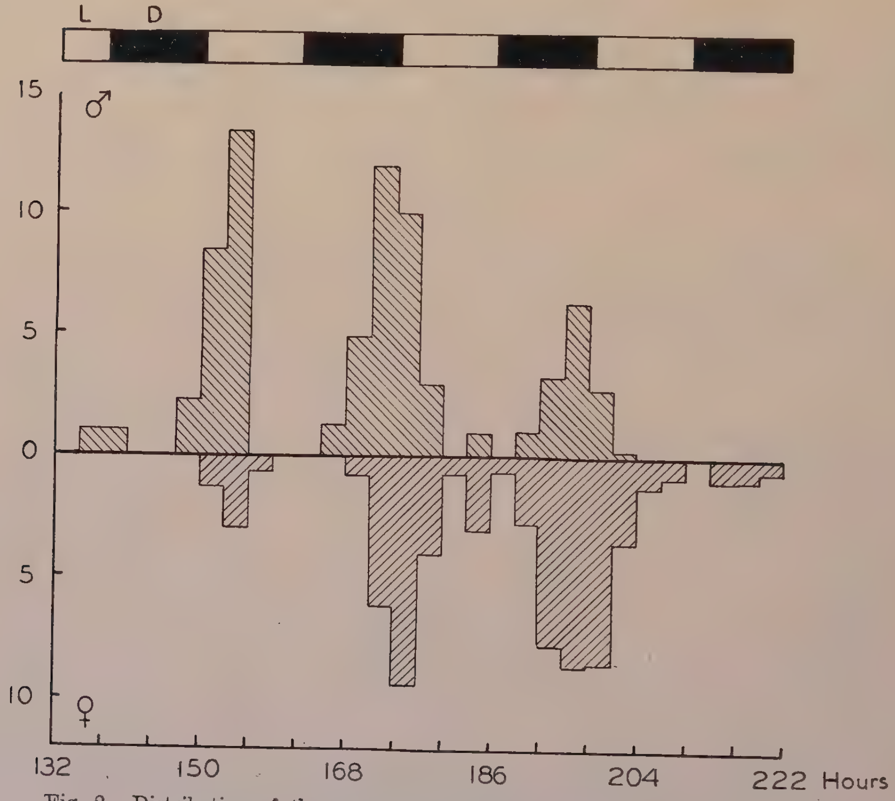


Fig. 2.—Distribution of the emergence of male and female imagines of *Aëdes taeniorhynchus* hatched simultaneously from the eggs.

From fig. 2 it will be seen that the females within each maximum emerged a little later than the males, which is probably normal. The difference is, however, so small that it was not always discernible in material analysed by 3-hour intervals. It is most likely that it is the difference between males and females in the duration of the pupal stage, as mentioned above usually 1 to 2 hours, which causes this delay in the appearance of the females during the daily emergence maxima.

Conclusions.

The tentative conclusions which may be drawn from these preliminary experiments are the following. The duration of larval life in *Aëdes taeniorhynchus* is determined by temperature and nutrition, pupation occurring ordinarily around the change from day to night. But it must be borne in mind that the critical moment when the process of transformation begins must precede the moment of pupation (*i.e.*, actual casting of the last larval skin) by an unknown number of hours. When the process is once started it seems to continue unremittingly to the emergence of the adult, and at a rate influenced only by temperature.

If the temperature of the water in the pools in which the larvae are living in the field is known, it should be possible to predict at what hour of the day the emergence maxima will take place. This hour is probably of some importance from the viewpoint of applied entomology, because unpublished observations suggest the possibility of a certain relationship between the hour of emergence, the hour when the migration starts, and, possibly also, the range of migration.

Summary.

A series of field observations and rearing experiments were carried out in Florida to gain information on the duration of the larval stage and the time of day of pupation and emergence of the salt-marsh mosquito, *Aëdes taeniorhynchus* (Wied.).

The technique ~~adopted~~ in a series of experiments is described.

It was found that the duration of the larval stage is dependent on several factors of which water temperature is probably the main factor. Hunger was also shown to be important either through lack of food or overcrowding. Larvae which later became male adults pupated before those which became female imagines.

The period of maximum pupation is determined by the distribution of light and darkness, 83 per cent. of all pupation taking place during the evening periods, 15 to 24 hours after experimental midnight, and 48 per cent. in the period just after sunset, 18 to 21 after experimental midnight. The tendency to pupate around sunset is thought to have just as much accelerating as retarding effect on the larval development.

Temperature is considered to be the only factor of importance in determining the duration of the pupal stage which varies from 61 hours at 20·8°C. to 45 hours at 25·5° and 37 hours at 29°.

Both in nature as well as under controlled conditions in the laboratory it was found that, for a large number of larvae hatched simultaneously, the emergence of adults usually lasts three or fours days, with a maximum at the same hour on each of these days. The period of emergence is proportional to the duration of the post-embryonic development and may under unfavourable conditions last weeks.

Maximum emergence of imagines has been found to occur at various times of the day. This is as should be expected since the hour of pupation is fixed to a certain period of the day, and the duration of the pupal stage is solely dependent on the temperature.

The difference in the duration of pupation in males and females is very small but owing to the rather marked sexual difference in the duration of the larval stage, 129 hours for males against 145 for females at 29°, there is a

preponderance of males during the first emergence maxima and of females in the last.

It is concluded that if the temperature of the water in which the larvae are living in the field is known, it should be possible to predict at what hour of the day the emergence maxima will take place.

GALL-MIDGE LARVAE AS ENDOPARASITES, INCLUDING THE DESCRIPTION OF A SPECIES PARASITISING APHIDS IN TRINIDAD, B.W.I.

By H. F. Barnes.

Entomology Department, Rothamsted Experimental Station.

The great plasticity of the gall midges (Cecidomyidae) and the success of their larvae in establishing themselves in a great variety of food niches is well known. In addition to the great diversity of feeding haunts among the phytophagous forms, one has only to recall their record as predators of Aphids, Coccids, mites and so on. It seems therefore somewhat surprising that so few are known to be endoparasites.

It is the purpose of this paper to stimulate interest in such forms by reviewing the available information and at the same time presenting the description of a new endoparasite of Aphids that has recently been discovered in the West Indies. Immediately following this paper is one (Kirkpatrick, 1954) in which Professor Kirkpatrick notes the new midge's hosts and distribution, and describes its biology.

Review of Gall-midge Larvae as Endoparasites.

Only three such species belonging to two genera have been described up to the present, although a few other unidentified species have been found.

The first recorded instance of endoparasitism by larvae belonging to this Dipterous family is that of *Endaphis perfidus* Kieffer from Lorraine (Kieffer, 1896, 1901). The female of this species was noticed by Kieffer laying its bright red eggs singly on the backs of apterous *Drepanosiphum platanoides* (Schr.) on the undersides of the leaves of *Acer pseudoplatanus*. The larva, which was bright red and thus visible in the green Aphid by transparency, possessed a well-developed sternal spatula and apparently spent the whole of its feeding period inside the abdomen of its host. Although Kieffer did not see how the newly hatched larva penetrated the Aphid, he did observe that the full-grown larva left it by the anal aperture. The larva~~e~~ then projected itself into the air and "jumped" in the manner of *Contarinia* larvae thus falling to the soil in which it pupated. Kieffer added that there were several generations a year. Nothing further of importance seems to have been published concerning this species, although Bagnall & Harrison (1918) reported finding it in Northumberland.

As far as the present author is aware the type of *E. perfidus* was lost together with Kieffer's other types, but typical specimens, donated to the late Dr. E. P. Felt by Kieffer and used by him in drafting a generic description of *Endaphis*, are in the Felt collection of gall midges. I have been recently informed (*in lit.*, 25.5.54) by Richard H. Foote, of the U.S. Dep. Agric. Entomological Research Branch, Washington, D.C., that there are three specimens, 2 ♂♂ and 1 ♀, with wings of two of these mounted separately. Mr. Foote has the Felt collection of gall midges on loan for the next five years from the New York State Museum. The re-discovery of this species and the preservation of specimens is highly desirable. Incidentally not one of the three species originally described by Felt in the genus *Endaphis* was endoparasitic, nor even associated with Aphids, and all have been later transferred from the genus *Endaphis* to other genera.

There are apparently only two additional published records concerning gall midges endoparasitic in Aphids. One is merely a statement by Bagnall & Harrison (1918) that the larva of an *Endaphis* sp. was found in an *Aphis* on *Ononis repens* in Durham. The other is a short paper by Hennig (1941) dealing with an *Endaphis* cf. *perfidus* Kieffer that was reared by Speyer, who had found the larvae living as endoparasites in *Macrosiphum jaceae* (L.) on *Carduus* at Stade on 6th August 1940. The larvae pupated in the soil and the midges emerged on 24th August the same year. Hennig figured the palps of the male, some of the flagellar segments of both sexes, the male genitalia, the distal tarsal segment and scales from the palps, wing and tarsal segment, but he did not actually name the species, being content to refer to it as *Endaphis* (cf. *perfidus* Kieffer).

From correspondence with Dr. W. Speyer and Prof. Dr. H. Sachtleben I have been able to ascertain that 4 slides (3 ♂♂, 1 ♀) and a tube of adult midges reared by Speyer are preserved in the Deutsches Entomologisches Institut, Berlin. Through the kindness of Prof. Sachtleben I have been able to examine the tube of specimens and retain 1 ♂ (Cecid. 9288) and 4 ♀♀ (Cecid. 9289–92) in the Barnes collection, thus leaving 32 specimens in the tube.

The second species of gall midge recorded as an endoparasite is *Endopsylla agilis* de Meijere, three slides of which are preserved in the Entomologische Museum, Amsterdam. Mr. W. Nijveldt has kindly informed me that two of these each bear a female midge while on the third there is part of a larva. Since Venetian turpentine was used as the mountant the specimens are now very transparent.

The larvae of *E. agilis* were found living inside adult winged *Psylla foersteri* Flor on alder in the Netherlands (de Meijere, 1907). Although de Meijere once found four midge larvae in a single *Psylla*, more often he found only one. When fully grown the larvae left their host and pupated in the soil. De Meijere was successful in rearing one male and four females. On these he based his description of the genus and species, figuring the wing, the two distal flagellar segments of the male, the male genitalia, the anal segment and the well-developed sternal spatula of the larva. No mention was made of the larva being endowed with the power of "jumping", neither did de Meijere discover where the eggs were laid although he pointed out that the midge's ovipositor was not of the piercing type. Bagnall & Harrison (1924) recorded this species from Northumberland.

The third species of endoparasitic gall midge seems to be the most specialised yet known, being the only one yet known to pupate inside its host. This is *Endopsylla endogena* (Kieffer) the type of which has presumably been lost with Kieffer's other types. It was found by Tavares in the larva of *Stephanitis pyri* (F.) in Portugal and sent to Kieffer for determination. Only a single male was reared by Kieffer who described it and the pupa (Kieffer, 1907). Pupation, as already mentioned, occurred inside the dead Tingid and emergence took place through a circular hole in the back of the host. Apparently this species has never been found again.

More information however is available concerning gall midges as endoparasites of Psyllids, thanks to the investigations of Lal and Speyer. Lal (1934), working on Psyllids in Scotland, found in *Psylla mali* (Schmidb.), *P. pyricola* Foerst. and *P. melanoneura* Foerst. what at the time was considered to be a new species of *Endopsylla* but now is thought, pending an examination of de Meijere's specimens of *E. agilis*, to be most probably *E. agilis*. Between 20 and 40 per cent. of *P. mali* race *peregrina* Foerst. on hawthorn were found to be parasitised. Such Psyllids became swollen and sluggish, quickly losing their power of jumping but not changing their colour. Lal discovered that the eggs were laid singly on one or other of the fore wings of the Psyllids, although occasionally two or three could be found on a wing and sometimes even both wings bore eggs. Eggs were first noticed early in June and were found as late as the middle of August. It may be noted that the late G. Fox Wilson and the author have found the eggs of this midge on Psyllids swept from hawthorn hedges at Wisley and Harpenden respectively, thus indicating a somewhat widespread distribution of this species.

Lal found that the eggs took 6–13 days to hatch and that the larvae first fed for 3–4 days as ectoparasites. Then they burrowed through one of the intersegmental membranes into the haemocoele of the Psyllid. After 6–12 days inside the host the larvae left by piercing the abdomen at its base. Then, after remaining a day or two on the hawthorn leaves, they dropped to the soil where they spent about 6 days as pupae. Lal considered that there were two generations a year.

Specimens of males of this species of *Endopsylla* (Cecid. 2145–6), females (Cecid. 2147 and 2932) and larvae (Cecid. 2049–51) were kindly presented by Lal to the Barnes collection of gall midges. In addition, this collection contains eggs (Cecid. 2933–4) *in situ* on the wings of the hawthorn Psyllid collected at Harpenden on 2nd August, 1933.

Speyer (1929) first mentioned the existence in Germany of an unidentified gall midge whose red eggs were to be found on the wings of *Psylla mali* (Schmidb.) on apple and whose larvae lived as endoparasites. Later he (1941) found that on the average 19 per cent. of the adults of *P. mali* on apple in the hilly ground near the sea coast between the Elbe and Weser were parasitised by an *Endopsylla* which he thought was probably *E. agilis* de Meijere. Speyer stated that the eggs were usually found on the wings, that the larvae hatched in 14 days' time and later dropped to the ground. Pupation took place on the surface of the soil and lasted at least 6 days. He stated that, since eggs could be found from June to September and the first mature larvae in late June, there were possibly two generations a year. It may be noted that Speyer's observations concerning this midge's biology correspond closely with those made by Lal on the gall midge he studied in Scotland.

From correspondence with Dr. W. Speyer and Prof. Dr. H. Sachtleben I have been able to ascertain that 3 slides (1 ♂, 2 ♀ ♀) and a tube of adult midges of Dr. Speyer's material are preserved in the Deutsches Entomologisches Institut, Berlin. Through the kindness of Prof. Sachtleben I have been able to examine the tube of specimens and retain 1 ♂ (Cecid. 9293) and 3 ♀ ♀ (Cecid. 9294–6) in the Barnes collection, thus leaving 8 specimens in the tube.

In order to complete this review it should be mentioned that V. F. Eastop has discovered gall-midge larvae in the bodies of apterous *Chaitophorus* (*Pseudomicrella*) sp., cf. *salicti* (Schr.) collected on *Salix alba* during late June 1952 at Gulpen, Limberg, Netherlands. These larvae are without much doubt those of an *Endaphis* sp. At the same time, in the same locality, he also found larvae that also appear to be *Endaphis* sp. in a colony of *Aphis farinosa* Gmel. (syn. *A. saliceti* Kalt.) on *Salix caprea*. This discovery and preservation of *Endaphis* sp. larvae is most valuable. It remains now for someone to rear some midges from such larvae. While Aphids are being studied so much it should be quite possible for this to be done.

Mr. Eastop has kindly presented to the Barnes collection the four slides he made; two of these (Cecid. 9284–5) each bear one of the apterous *Chaitophorus*, each of which contains a gall midge larva inside the Aphid or in the act of leaving it; the other two (Cecid. 9286–7) each bear one of the larvae found in the colony of *A. farinosa*.

The Species parasitising Aphids in Trinidad.

Thanks to the courtesy of Professor T. W. Kirkpatrick I have had the privilege of examining the gall midge he has been studying in Trinidad. I have also been able to enrich the Barnes collection by incorporating males, females, larvae, including two that I dissected from their hosts, and parasitised *Toxoptera aurantii* (Boy.), all of which he sent me.

One of the more interesting features of this gall midge is that, although superficially reminiscent of the only other described gall-midge endoparasite of Aphids, *Endaphis perfidus*, because its wings are thickly clothed with narrow scales and because its larvae " jump ", it belongs to the Trifila group of the CECIDOMYIDAE, whereas *E. perfidus* is a Bifila. It must not be thought, however, that " jumping " larvae are restricted to the Bifila; such larvae also occur among the Trifila, *e.g.*, the recently described *Camptodiplosis auriculariae* (Buxton & Barnes, 1953).

In Felt's key to genera of the world it falls, because of its claws being simple or not toothed on any of the legs, the quadriarticulate palps and the third vein uniting with the margin before the apex of the wing, among a small group of genera most of whose species are known to be predatory on mites or Coccids. All these genera, *e.g.*, *Arthrocnodax* Rübsaamen, *Adelgimyza* Del Guercio, *Cecidomyella* Del Guercio and *Silvestrina* Kieffer, except one have hyaline wings. The exception, *Chrysodiplosis* Kieffer of which incidentally nothing is known concerning the larval habits since only a solitary male was caught in the Seychelles, has the wings densely covered with brown hairs, the costa being covered with black scales; the dorsal part of the thorax is clothed with yellow scales and there are denticulate long hairs on the flagellar antennal segments. The gall midge from Trinidad has none of these conspicuous characters and, furthermore, it cannot be placed among the preceding genera because its wings are covered with narrow scales.

Endopsylla, the only other gall-midge genus whose members are known to be endoparasites in addition to *Endaphis*, falls in the next group of genera in which the third vein unites with the costa at the apex of the wing. The wings are densely clothed with hairs, not scales, and in the female the basal portion of the first flagellar segment of the antenna is distinctly longer than that of the second and its neck is considerably longer than wide, whereas in the female of the Trinidad gall midge the basal portions of the first and second flagellar segments are about equal and the neck of the first is transverse. In addition, there are other characters that prevent the gall midge reared by Professor Kirkpatrick being placed in the genus *Endopsylla*.

It is considered expedient therefore to erect a new genus to contain the Trinidad gall midge. The name *Pseudendaphis* is suggested as recalling its habit of parasitising Aphids and indicating its differentiation from *Endaphis*, the only other gall-midge genus containing Aphid endoparasites.

Pseudendaphis, gen. n.

A typical Trifila of the CECIDOMYINAE in which the claws are simple on all the legs, the palps have four segments and the third vein reaches the margin slightly before the apex of the wing. The membrane of the wings is thickly clothed with narrow scales. In addition to the more usual long thin setae on the flagellar segments of the antennae there are in both sexes two dense whorls of almost broad and exceptionally straight dark setae. There are scales on the dorsal part of the thorax and the abdomen, especially in the female, is thickly clothed dorsally with dark scales and hairs. The upper lamella of the male genitalia has a comparatively shallow V-shaped emargination, while the lower lamella is broad and entire. The ovipositor is lamelliform, each lateral lamella bearing two conspicuous stout setae.

Pseudendaphis maculans, sp. n.

Male. Length about 1 mm. Antennae: 2 + 12; proximal segment pale and slightly overlapping the second with what might be termed a slight tooth (Cecid.

9267), second segment globular, as dark as the flagellar segments; 1st and 2nd flagellar segments fused; each flagellar segment with subglobular basal node bearing one circumfilum with loops of moderate length and a dense whorl of exceptionally straight almost broad dark setae separated by a short stem from the distal node that is slightly elongated and constricted between the proximal narrower and the wider distal portions; the distal node of each segment bears proximally one circumfilum mingled with long thin setae and just distal to the constriction another circumfilum rather concealed by a second dense whorl of exceptionally straight almost broad dark setae; the loops of the three circumfila are approximately the same length; each flagellar segment except the 12th terminates in a short neck; the stem and neck on the 1st flagellar segment are almost transverse, those of the 3rd are about as broad as long, more distally they are about twice as long as broad; on the 12th flagellar segment the distal prolongation is setose distally but the proximal portion is bare thus resembling a neck. Palps: 4 segments; the proximal one small, quadrate; the second and third about two-and-a-half times as long as broad; the fourth slightly longer but about the same width. General colour of thorax and abdomen rather dark brown, bearing scales and long hairs; the almost black spot in the abdomen characteristic of predatory midges is once again present. Wings: thickly clothed with dark narrow scales, rather wide; 3rd vein interrupting margin just before apex of wing; 5th vein forked; all veins scarcely visible when most of the scales are present. Legs dark brown, thickly clothed with dark hairs and narrow scales, less so at joints; claws all simple, moderately curved; empodium nearly as long as claws. Genitalia: basal clasp segment moderately slender with no inner lobe; distal clasp segment long, rather swollen at base but soon becoming slender; dorsal lamella rather shallow V-shaped emargination, each lobe roundly triangular; lower lamella broad, entire; the lower lamella extends about half way up the basal clasp segment, the upper lamella slightly further and the somewhat stout style the full length of the basal clasp segment.

Type: Cecid. 9265 (in the Barnes collection).

Paratypes: Cecid. 8483–8 and 9266–7.

Female. Slightly bigger than male. Antennae: proximal segment pale, second dark, same colour as flagellar segments; each flagellar segment (except the 12th) consisting of a cylindrical basal portion and a short neck; basal portion of 3rd just over twice as long as broad, neck transverse; basal portion of 10th about the same length and proportions, but neck about twice as long as broad; 12th flagellar segment about the same size and proportions, no prolongation (or neck); basal portion of each flagellar segment slightly constricted medially, adorned with two dense whorls, one proximal, the other distal, of exceptionally straight almost broad dark setae, between these whorls are the usual long thin setae; circumfila applied. Palps: about as in male. Abdomen: thickly clothed with dark scales and hairs; ovipositor lamelliform, each lateral lamella bearing two stout setae distally. Otherwise about as in male.

Type: Cecid. 8489 (in the Barnes collection).

Paratypes: Cecid. 8490–2 and 9268–9.

Larva. Full grown about 1 mm. in length; well developed roundly bifid sternal spatula. In life: when full grown lies bent up in U-shape or J-shape in abdomen of apterous *Toxoptera aurantii* (Boy.) and " jumps " to soil at maturity. Cecid. 9270–2 (the latter two extracted from *T. aurantii*).

Type locality: Trinidad, B.W.I.

The specific name *maculans* has been chosen to designate this species, on the suggestion of Prof. Kirkpatrick, because a parasitised Aphid assumes a characteristically spotty appearance (see Kirkpatrick, 1954, p. 779).

A tube containing 6 specimens (♂♂ and ♀♀) of *P. maculans* has been presented to the Deutsches Entomologisches Institut, Berlin, in exchange for the specimens of *Endopsylla ? agilis* and *Endaphis* (cf. *perfidus* Kieffer) given to the Barnes collection.

Summary.

A review of the available information concerning gall midges as endoparasites shows that only three species in two genera have been described.

Endaphis perfidus Kieffer is a parasite of apterous *Drepanosiphum platanoides* (Schr.) (APHIDIDAE) in Lorraine and England. Although on several occasions larvae of *Endaphis* sp. have been found in England, the Netherlands and Germany parasitising other Aphids, practically no information additional to that supplied by Kieffer has been published. In only one instance besides *E. perfidus* has the adult midge been reared and figured, *i.e.*, *Endaphis* (cf. *perfidus* Kieffer) in *Macrosiphum jaceae* (L.) on *Carduus* in Germany.

Endopsylla agilis de Meijere is a parasite of winged *Psylla foersteri* Flor (PSYLLIDAE) in the Netherlands. The bionomics of what is almost certainly the same species, parasitising *P. mali* race *peregrina* Foerst. on hawthorn (also *P. pyricola* Foerst. and *P. melanoneura* Foerst.) and *P. mali* (Schmidb.) on apple, respectively, have been studied in Scotland and Germany.

Endopsylla endogena (Kieffer) was found parasitising the larva of *Stephanitis pyri* (F.) (TINGIDAE) in Portugal but has not been recorded again.

A fourth species, *Pseudendaphis maculans*, gen. et sp. n., that parasitises various Aphids in Trinidad, has now been described.

Indications are given of the whereabouts of any existing types or other specimens of all the known endoparasitic gall midges.

References.

BAGNALL, R. S. & HARRISON, J. W. H. (1918). A preliminary catalogue of British Cecidomyidae (Diptera), with special reference to the Gall-midges of the North of England.—Trans. ent. Soc. Lond., **1917,** pp. 346–426.

BAGNALL, R. S. & HARRISON, J. W. H. (1924). New British Cecidomyiidae. 5.—Ent. Rec., **36,** pp. 36–38.

BUXTON, P. A. & BARNES, H. F. (1953). British Diptera associated with fungi. I. Gall Midges (Cecidomyidae) reared from the larger fungi.—Proc. R. ent. Soc. Lond., (B) **22,** pp. 195–200.

HENNIG, W. (1941). Neues über parasitische Dipteren (Cecidomyiidae and Chloropidae).—Arb. morph. taxon. Ent., **8,** pp. 196–200.

KIEFFER, J. J. (1896). Observations sur les *Diplosis*, et diagnoses de cinq espèces nouvelles (Dipt.).—Bull. Soc. ent. Fr., **1896,** pp. 382–384.

KIEFFER, J. J. (1901). Monographie des Cécidomyides d'Europe et d'Algérie.—Ann. Soc. ent. Fr., **69** (1900), pp. 181–472.

KIEFFER, J. J. (1907). Eine neue endoparasite Cecidomyide.—Z. Hymen. Dipt., **7,** pp. 129–130.

Kirkpatrick, T. W. (1954). Notes on *Pseudendaphis maculans* Barnes, a Cecidomyid endoparasite of Aphids in Trinidad, B.W.I.—Bull. ent. Res., **45**, pp. 777–781.

Lal, K. B. (1934). Insect parasites of Psyllidae.—Parasitology, **26**, pp. 325–334.

de Meijere, J. C. H. (1907). Eerste supplement op de Nieuwe naamlijst van Nederlandsche Diptera.—Tijdschr. Ent., **50**, pp. 151–195.

Speyer, W. (1929). Der Apfelblattsauger *Psylla mali* Schmidberger.—Monogr. PflSch., no. 1, 127 pp.

Speyer, W. (1941). *Endopsylla ? agilis* de Meijere (Cecidomyidae) als Entoparasit von *Psylla mali* Schmidb.—Arb. physiol. angew. Ent., **8**, pp. 39–41.

NOTES ON *PSEUDENDAPHIS MACULANS* BARNES, A CECIDOMYID ENDOPARASITE OF APHIDS IN TRINIDAD, B.W.I.

E.H

By T. W. Kirkpatrick.
Imperial College of Tropical Agriculture, Trinidad, B.W.I.

Hosts of *Pseudendaphis maculans* Barnes and their Distribution.

Toxoptera aurantii (Boy.).

This is a common species on cacao in Trinidad and large colonies are usually parasitised to a greater or lesser extent. I have found the parasite almost wherever I have found this Aphid, in most of the cacao-growing valleys in the Northern Range, and in the Central Range. *T. aurantii* is not common on *Citrus* in Trinidad, but the only colonies seen, on a single grapefruit tree in the grounds of the Imperial College of Tropical Agriculture, were heavily parasitised.

Pentalonia nigronervosa Coq.

On bananas I have only seen small colonies of this Aphid, well concealed at the base of young leaves or in the unfolded whorl, and no parasites have been found in them. One large colony has, however, been found on the leaf-stalks of tannia (*Xanthosoma sagittifolium*) in the Arima valley, and this was very heavily parasitised.

Aphis gossypii Glov.

This is a fairly common species on *Citrus* and, among numerous colonies in a *Citrus* orchard on I.C.T.A.'s New Farm, several have been found in which a few were parasitised, but none in which the percentage of parasitism approached that frequently seen in colonies of *T. aurantii*. *A. gossypii* is also common on egg-plant (*Solanum melongena*) and various cucurbits, but parasites have not been observed in Aphids on these host-plants.

Aphis craccivora Koch (*leguminosae* Theobald).

This is an abundant species on *Gliricidia sepium* but though numerous colonies have been examined no parasitised ones have been found on this host-plant. Where, however, *Gliricidia* is used as a shade for cacao, *A. craccivora* often occurs on the cacao, sometimes in pure colonies and sometimes mixed with *T. aurantii*. In one such mixed colony, which contained several parasitised *T. aurantii*, there were two parasitised apterae of *A. craccivora*, but it is clear that it is not a normal host.

Abundance.

P. maculans occurs throughout the year but is commoner in the dry season. This may be due to the relative scarcity of large colonies of *T. aurantii* during the wet season when, as a rule, entomogenous fungi reduce the size of the colonies.

Colonies comprising a hundred or more apterae on one or a few adjacent leaves are sometimes parasitised to the extent of 50 per cent. or more. Small colonies frequently escape parasitism altogether, though some have been found consisting of only 25 or fewer apterae, all of which were parasitised.

The percentage of alates in colonies of *T. aurantii* is very variable, from 0 to, rarely, over 70, but there is a remarkable difference in the proportions of apterae and alates that are parasitised. The following figures will serve to give some idea of this difference. (Nymphs too young to show either traces of wing-buds or visible signs of being parasitised (see below) at the time of collection are not included, nor are colonies in which no alates were present.)

	Total number of		Visibly parasitised on day of collection	
	Apterae	Alates	Apterae	Alates
Dry season				
I.C.T.A., March 1953 .. .. .. Several small colonies on one tree	226	32	100	0
I.C.T.A., March 1953 .. .. .. One large colony	750 (approx.)	250 (approx.)	74	3
I.C.T.A., March 1953 .. .. .. One colony	107	13	69	0
Diego Martin, April 1953 .. .. Two colonies on one tree	300 (approx.)	180 (approx.)	95	5
Wet season				
I.C.T.A., July 1953 .. .. .. One colony	71	228	23	1
I.C.T.A., July 1953 .. .. .. One colony	75	77	14	0
Diego Martin, July 1953 .. .. Several small colonies	121	7	40	1
Total	1,650	787	415	10

Thus 25 per cent. of the apterae were parasitised, compared with little more than one per cent. of the alates.

A similar difference was observed in the single large colony of *P. nigronervosa*, in which 449 apterae and 27 alates were parasitised. The proportion of apterae to alates in this colony was roughly estimated at four to one.

All except two of about fifty parasitised specimens of *A. gossypii* that have been collected were apterae.

Since it is improbable that the female parasite could attack those Aphids that will become apterae to a greater extent than those that will be alates (for at the time of attack no external trace of wing-buds is evident) it is likely that the developing parasite larva somehow inhibits wing formation. The comparatively few parasitised Aphids that do become alates are, perhaps, attacked at a later stage than usual, when wing development has already been determined. According to Rivnay (1937) the turning-point in the development of alates or apterae in *T. aurantii* takes place during the first two days of nymphal life.

Life-history.

I have been unable to observe the act of oviposition. When parasites were enclosed with Aphids in a tube they showed little interest in them except that they were occasionally seen apparently feeding on the waxy secretion from the cornicles. Large numbers of adult parasites have been put in small cages containing *T. aurantii* on young, growing cacao plants and *P. nigronervosa* on banana seedlings but, though some of the parasites remained alive for a week, none of the Aphids became parasitised. It is, however, very difficult to establish healthy colonies of these Aphids in cages, largely owing to entomogenous fungi, and very few of them survived long enough to show visible signs of being parasitised.

A parasitised Aphid assumes a characteristic spotty appearance (fig. 1) about 36 hours before the parasite larva leaves its body. This is due to the integument becoming much paler and more transparent than in a healthy Aphid, and to the formation of numerous irregularly-shaped accumulations of reddish brown granular matter, readily visible through the integument on both the dorsum and venter. These may possibly consist of the excreta of the earlier stages of the parasite larva, though shortly before it is due to leave the Aphid the gut is full of dark excremental matter which is not voided until just before pupation. Or possibly it is interference with the normal physiological function of the host that causes both the accumulations of dark matter and the transparency of the integument.

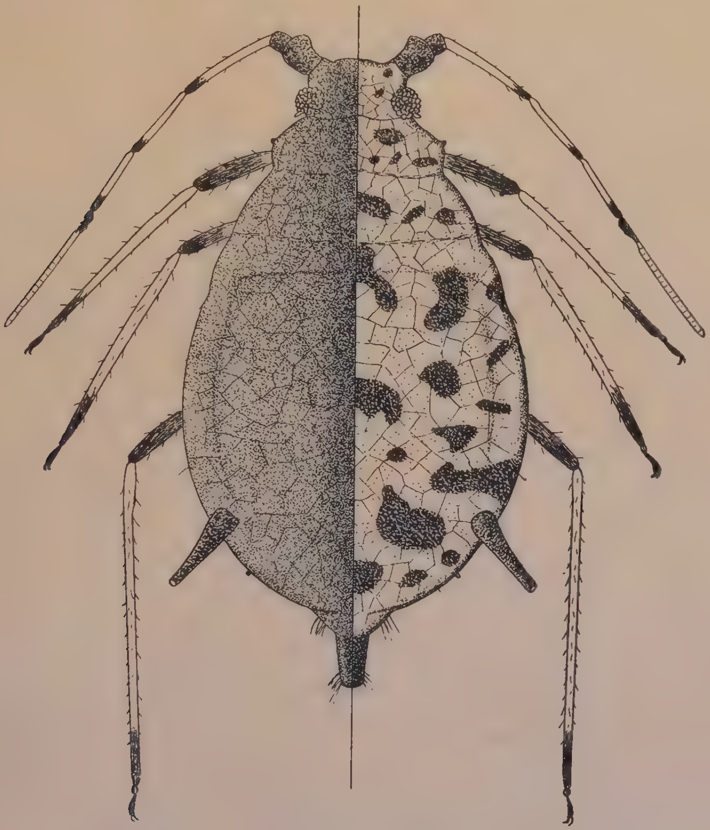


Fig. 1.—*Toxoptera aurantii* (Boy.). Apterous adult: left side, normal; right side, parasitised by Cecidomyid.

The appearance of the other three species of Aphids in which the parasite has been observed is very similar to that of *T. aurantii*, except that in *A. gossypii* the spots are dark green.

The majority of apterae assume the "spotty" appearance when in the last nymphal instar, though some not until adult, and some in the penultimate nymphal instar. A nymph that has become "spotty" has never been observed to moult.

I have seen only a single parasitised adult alate of *T. aurantii* and none of *A. gossypii*, but of 27 parasitised alates of *P. nigronervosa* 12 did not turn "spotty" until they became adult.

Only one parasite larva develops in each host. No parasitised Aphid has produced young, though in two (out of at least fifty) adult apterae that have been dissected when "spotty" a well-developed egg has been found.

Parasitised Aphids are not rejected by the larvae of Coccinellidae and Syrphidae.

The time spent by the parasite larva in the body of the Aphid is about 6–7 days, as deduced from the following observations.

(1) Part of the large colony of *P. nigronervosa* mentioned above was kept under observation in the laboratory and all "spotty" Aphids removed daily. Five days after collection the appearance of "spotty" Aphids ceased.

(2) From several heavily parasitised colonies of *T. aurantii* a number of unspotted nymphs was removed and placed on flush leaves of young cacao plants growing in pots, being roughly graded by size into three groups. To reduce mortality from fungi no cages were put over the plants and many of the Aphids were lost. However, from the smallest sized group, consisting of first- and probably some second-instar nymphs, eight out of 20 survivors became "spotty" five days after collection but no more subsequently. The larger, third- and fourth-instar nymphs that became "spotty", did so 1 to 3 days after collection, so it is concluded that they are normally attacked during the first and possibly also the second stadium. Larvae 0·25 mm. long have been dissected from second-instar nymphs.

I have examined a considerable number of Aphids in parasitised colonies but have never seen a parasite larva feeding externally, so it seems probable that there is no prolonged ectoparasitic existence as there is with *Endopsylla* sp. (Lal, 1934).

Shortly before leaving the Aphid and at least 24 hours after the latter has become definitely "spotty", the parasite larva turns pink, its mid-gut is filled with black excremental matter, and it is visible through the integument of the Aphid. It makes its way out of the abdomen of the Aphid, which dies very shortly, and reaches the ground. It is then about 1·5 mm. in length. Like the larvae of many Cecidomyidae it is capable of leaping a considerable distance, sometimes as much as 10 cm. When given access to damp soil and trash in the laboratory, it soon burrows in, though it does not pupate for about two days. The pupa is pink, and is not enclosed in a cocoon. Nine or ten days after leaving the host the adult emerges, always in the afternoon between 1330 and 1630 hr., and the majority about 1500 hr.

T. aurantii is not a serious pest of cacao in Trinidad. It is largely controlled in the dry season by Coccinellidae and Syrphidae (*Baccha* spp.) and in the wet season also by entomogenous fungi, but this Cecidomyid undoubtedly contributes to its control at any rate in the dry season.

It may be remarked that no Hymenopterous parasites of any species of Aphid have been recorded from Trinidad.

Summary.

An account is given of the life-history of *Pseudendaphis maculans* Barnes, a common and widely distributed endoparasite of Aphids, especially of *Toxoptera aurantii* (Boy.), in Trinidad. Alates are parasitised to a much smaller extent than apterae: it is thought that this is due to the parasite larva inhibiting wing

development. Nymphs appear to be attacked usually during the first stadium; the parasite larva is fully fed after 6 to 7 days. Shortly before the larva leaves its host the latter assumes a characteristic spotty appearance, due to numerous granules of dark matter that are readily visible through the integument, which has become paler and more transparent than normal. Pupation takes place in the soil: 9–10 days after leaving the host the adult emerges, invariably during the early afternoon.

Acknowledgements.

I am indebted to Dr. H. F. Barnes for describing this parasite (see preceding paper).

References.

Barnes, H. F. (1954). Gall Midge larvae as endoparasites, including the description of a species parasitising Aphids in Trinidad, B.W.I.—Bull. ent. Res., **45,** pp. 769–775.

Lal, K. B. (1934). Insect parasites of Psyllidae.—Parasitology, **26,** pp. 325–334.

Rivnay, E. (1937). Moisture as the factor affecting wing development in the Citrus Aphis, *Toxoptera aurantii*, Boy.—Bull. ent. Res., **28,** pp. 173–179.

MUSCIDAE OF MEDICAL INTEREST IN THE ANGLO-EGYPTIAN SUDAN.

By D. J. Lewis.
Entomologist, Sudan Ministry of Health.

The Anglo-Egyptian Sudan forms a large part of the north-eastern area of the Ethiopian Region and adjoins the Palaearctic Region. Most of the country covers the eastern parts of the two districts, the Savanna and Arid, of the Sudanese zoogeographical Province (fig. 1). The high, isolated Marra Mountains lie in this area and, judging by insects of medical interest, have an essentially Ethiopian fauna containing many species prevalent much farther south. In considering the Muscid flies we may regard the Marra Mountains as an outlier of southern damper regions, and the Red Sea Hills and coastal plain as an extension of the Somali Arid District. The greater part of the Sudan thus becomes the " Savanna and Arid area ", which is in general rather flat country between 300 and 800 metres above sea level.

The Sudan Muscid fauna includes many species which are widely distributed beyond the Ethiopian Region. All of the 14 forms of *Musca* in the Sudan are included in West's (1951) list of species found in the Ethiopian Region. Apart from the widely distributed *M. domestica vicina* Macq., three species have a largely Ethiopian distribution, eight occur largely in north Africa or the Palaearctic Region, and two occur widely in both these areas.

Although some of the Muscids mentioned are cosmopolitan species associated with man, a striking number of the species of this family are confined to the fringes of the country and do not extend into the vast " Savanna and Arid area ". They comprise 33 of the 64 species of genera other than *Musca*, *Lyperosia* and *Lispe*. These three genera contain 22 Sudan species, none of which is confined to the fringes of the country. The genera of *Orthellia*, *Dichaetomyia* and *Pyrellina* have a particularly restricted distribution. Several of the more widely distributed Muscids are known chiefly from the far south or the Nuba Hills.

Discontinuous distribution is a feature of many Sudan insects. *Glossina tachinoides* Westw. is an outstanding example, and *G. morsitans* Westw. and some of the Marra Mountains species show considerable discontinuity.

Some of the species of *Musca*, and *Lyperosia spinigera* (Mall.), exhibit pale coloration in rather dry areas.

The Muscidae include, besides the well-known house-flies and biting and blood-drinking species, many flies which are much less important but are of some interest in relation to public health. Some of these may be mistaken for important species, and the larvae of various forms which breed in refuse, adults of which are received for identification from time to time, can be mistaken by public-health workers for those of *Musca*, and so can divert attention from the important species, whilst some larvae, which breed in refuse, kill or compete with those of *Musca*.

A number of species to be mentioned are metallic-green flies, some of which resemble *Lucilia*, and these and others are often found in fly traps. Certain of the species which breed in faeces may contaminate food, and some which feed on wounds may transmit pathogenic organisms.

No Muscids are known to cause myiasis in the Sudan except *Passeromyia heterochaeta* (Villen.), the larvae of which attack nestling birds.

Cattle trypanosomiasis in the absence of tsetse flies is an important problem over large areas of the grass plains of the Upper Nile, and Buxton (1949) has referred to the possible rôle of Muscids other than *Glossina* in transmission. He points out that most of the cases of trypanosomiasis are presumably due to "other biting flies" and that "it is important to accumulate facts about the distribution, life history, and seasonal incidence of the numerous biting flies (both

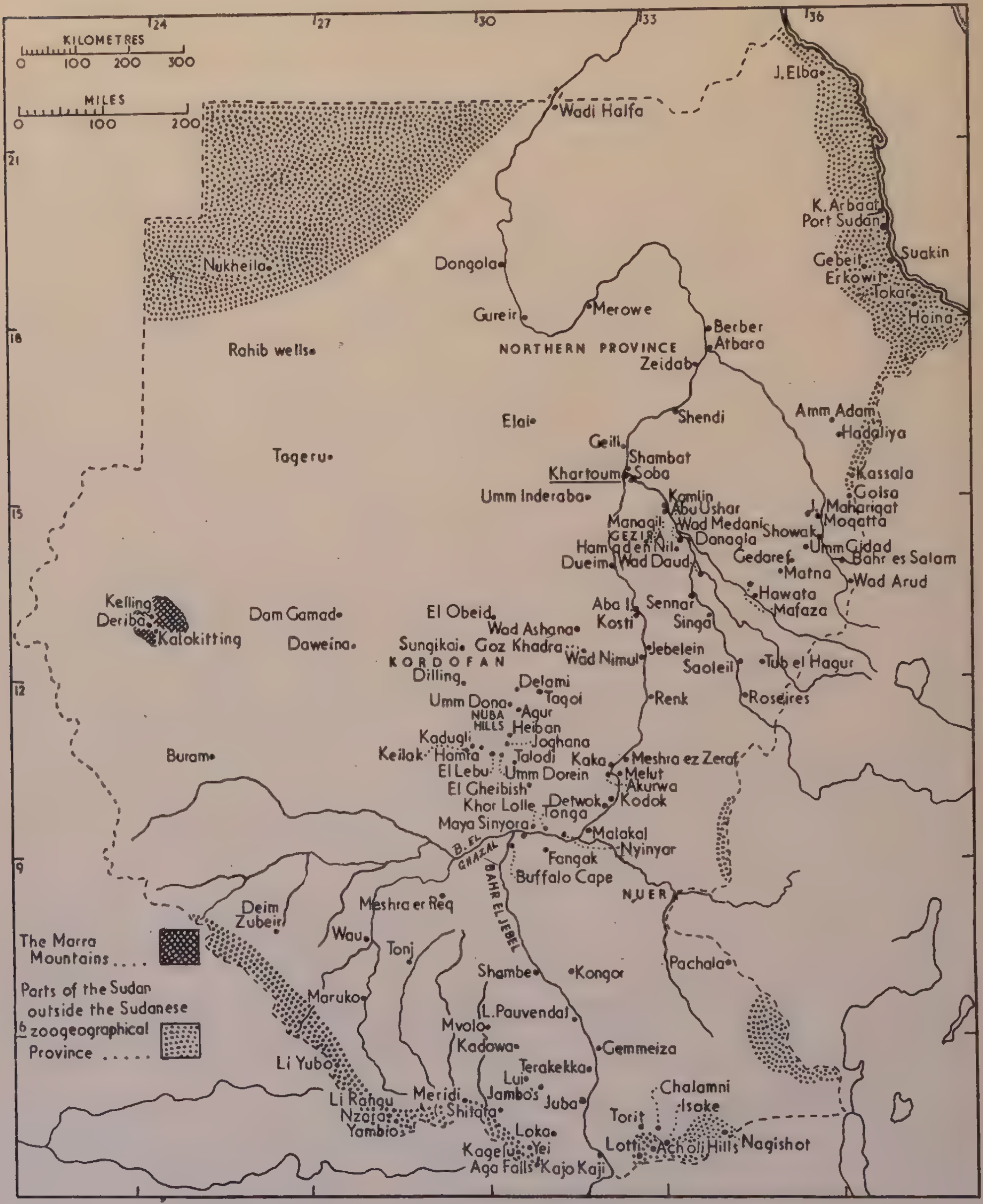

24
27
30
33
36
KILOMETRES
0 100 200 300
MILES
0 100 200
21
18
15
12
9
J. Elba
Wadi Halfa
K. Arbaat
Port Sudan
Suakin
Gebeit
Erkowit
Tokar
Hoina
Nukheila
Dongola
Merowe
Gureir
Berber
Atbara
NORTHERN PROVINCE
Zeidab
Rahib wells
Shendi
Amm Adam
Hadaliya
Elai
Geili
Shambat
Tageru
Khartoum
Soba
Kassala
Golsa
Umm Inderaba
Kamlin
Abu Ushar
J. Maharigat
Moqatta
Managil
Wad Medani
Showak
GEZIRA
Hamlad en Nil
Danagla
Umm Gidad
Dueim
Wad Daud
Gedaref
Bahr es Salam
Matna
Wad Arud
Hawata
Mafaza
Kelling
Deriba
Kalokitting
Dam Gamad
El Obeid
Aba I.
Sennar
Wad Ashana
Kosti
Singa
Daweina
Sungikai
Goz Khadra
Jebelein
KORDOFAN
Wad Nimul
Saoleil
Tub el Hagur
Dilling
Delami
Umm Dona
Tagoi
Renk
Roseires
NUBA HILLS
Agur
Heiban
Kadugli
Joghana
Buram
Keilak
Homra
Talodi
Kaka
Meshra ez Zeraf
El Lebu
Umm Dorein
Melut
El Gheibish
Akurwa
Khor Lolle
Detwok
Kodok
Tonga
Maya Sinyora
Malakal
B. EL GHAZAL
Nyinyar
Fangak
Buffalo Cape
NUER
BAHR EL JEBEL
Deim Zubeir
Meshra er Req
Wau
Tonj
Pachala
The Marra Mountains ....
Shambe
Kongor
Parts of the Sudan outside the Sudanese zoogeographical Province .....
Maruko
L. Pauvendal
Mvolo
Kadowa
Gemmeiza
Terakekka
Li Yubo
Lui
Chalamni
Jambo's
Juba
Isoke
Li Rangu
Meridi
Nzara
Shitata
Torit
Yambio
Loka
Kagelu
Yei
Lotti
Acholi Hills
Nagishot
Aga Falls
Kajo Kaji

Fig. 1.—The Anglo-Egyptian Sudan, showing places mentioned in the text. The extensive "Savanna and Arid area", as defined in the text, is unshaded.

TABANIDAE and *Stomoxys* and its near allies) ". He also points out that transmission by these biting flies cannot be regarded as a good general explanation of the situation because there are several areas in the south in which cattle trypanosomiasis appears to be strictly associated with tsetse belts and is absent from neighbouring districts where Tabanids, *Stomoxys* and other biting flies are abundant. It is thus possible that some one species of " other biting fly " has caused the outbreaks in the Upper Nile area. Buxton suggests that " the blood drinking Muscids (which cannot pierce the skin but feed at ulcers and other injuries) " should also receive attention.

The occasional spread of trypanosomiasis is probably increased by the movements of cattle induced largely by the attacks of TABANIDAE (Lewis, 1953). There is little doubt that biting Muscids are a contributory cause of these migrations.

The main object of this paper is to record the occurrence and known distribution in the Sudan of the important species of MUSCIDAE and those which for various reasons come to the attention of a medical entomologist. Several of the flies which have been found in houses only as occasional visitors have been omitted.

Some species probably occur much more widely than the distribution lists indicate. In these lists " J." indicates a jebel or hill and " K." a khor or water-course. The initials shown in parenthesis after certain records are those of the respective collectors, whose full names are given in the acknowledgements at the end of the paper.

Classification.

The following are some publications which deal with the classification of the MUSCIDAE:—MUSCIDAE in general, Colyer & Hammond (1951), Patton (1932, 1933, 1936), Patton & Gibbins (1934), van Emden (1941*a*, *b*, 1951); MUSCINAE, van Emden (1939), West (1951); STOMOXYDINAE, Malloch (1932), Patton (1933), Zumpt (1950); PHAONIINAE, van Emden (1942, 1943); COENOSIINAE, van Emden (1940); LISPINAE and FANNIINAE, van Emden (1941*b*).

MUSCINAE.

Alluaudinella.

Alluaudinella arguta (Karsch) occurs at Lotti, and *A. flaviceps* (Karsch) has been bred from dead snails at Wau.

Anaclysta.

This genus includes a species the larvae of which will eat full-grown larvae of *Musca* (Muirhead Thomson, 1947, referring to a species then included in *Gymnodia*). *Anaclysta eremophila* Br. & Berg. has been found at Wadi Halfa.

Ochromusca.

This genus has a superficial resemblance to *Auchmeromyia* and some other testaceous CALLIPHORIDAE. *Ochromusca trifaria* (Big.) occurs in the Koalib Hills and has been found in houses at Meridi, Kadugli (K.A.A.H.) and Yei.

Morellia.

Cuthbertson (1933) found a species of *Morellia* breeding in dung in Southern Rhodesia, and *M. bispinosa* Mall. feeding on dung, and Hammer (1941) reported that some European species fed on wounds and secretions of cattle. *M. bispinosa* occurs at Nagishot. *M. paradoxa* Villen. has been found at Fangak on an ulcer of a cow (P.A.B.), *M. prolectata* (Wlk.) (*abyssinica* Séguy) occurs at Lotti and Nagishot, and *M. smaragdina* Séguy at Jambo's.

Pyrellia.

Pyrellia scintillans Big. is known from Khartoum (bred from horse dung), Shendi and Wad Medani (bred from cow dung; adults caught in traps baited with rotting lucerne and with rotting cotton seed). *P. spinthera* Big. is known from Juba, Lotti and Terakekka.

Orthellia.

Several species of *Orthellia*, metallic flies not unlike *Lucilia*, occur in the Sudan. *O. albigena* (Stein) is widely distributed in Africa and occurs in the Sudan (van Emden, 1948*b*) at Deriba Lakes. It breeds in cow dung (Cuthbertson, 1932, 1934). *O. aureopyga* Mall. occurs at Nagishot, and *O. gemma* (Big.) (of which *O. artifrons* (Stein) is a synonym) at Li Yubu and Lotti (M.S.). *O. laxifrons* (Villen.) and *O. maculisquama* Villen. are known from Nagishot. *O. marginipennis* (Stein) has been found on rotting mangos at Yei. *O. nudissima* (Lw.) (*nigrocincta* Big.) is distributed from Aden to Natal and from the Sudan to Sierra Leone (van Emden, 1948*b*). Van Emden (1939) recorded it from the Sudan where it is known from Haina (R.C.M.-D.), Isoke, Lotti, Mvolo, Nagishot and Wad Medani. *O. racilia* (Wlk.) is known from Ikotos (M.S.), and *O. splendida* (Adams) from Yambio (C.E.W.).

Passeromyia.

Passeromyia heterochaeta (Villen.) is referred to by Cuthbertson (mentioned by Zumpt, 1951, and by Séguy, 1950). It occurs in Australia, China, India and most parts of Africa, and, in the larval stage, sucks the blood of nestlings of weaver birds (of which one species is an important pest of grain in the Sudan) and other species. In the Sudan it is known from Lui (in a house) and Nagishot, and from Wad Medani where many of its grass cocoons were found by Mr. F. W. Blake in nests of *Plesiositagra vitellinus vitellinus* (Licht.) in October 1952. Four nests were examined and one contained 22 puparia. This fly is probably common and widely distributed but is only noticed when it accidentally enters houses.

Musca.

Some breeding places of various species of house-flies.

Owing to the great importance of house-flies in the dissemination of disease, a considerable amount of information on their breeding places has been accumulated.

In the greater part of the Sudan warm dry weather prevails for most of the year and small amounts of refuse generally dry quickly when exposed to the sun. Balfour (1906) pointed out that in Khartoum house-flies increased in February and March before the hot weather of April. A similar increase in the middle of the dry season sometimes occurs at Wad Medani. On the coast, flies increase during the rainy season which occurs there in the winter.

Isolated human faeces.—Isolated deposits of excreta are an important source of house-flies on damp soil near rivers, but in dry open places in the central Sudan they tend to dry up quickly, although, as King (1908) remarked, *Musca* can breed in faeces and cow dung in spite of the hot dry conditions.

Pit latrines.—During 1940 a survey was made, in Omdurman and Khartoum North, of pit latrines which had various types of superstructure or none at all. A small sample of the contents of each pit was taken in a scoop and examined for larvae. In Omdurman, 1,165 pits were examined and it was found that most contained no fly larvae but 3·7 per cent. contained *Musca* larvae. In Khartoum North, 1,303 pits were examined and most were found to contain semi-aquatic fly larvae and 2·3 per cent. *Musca* larvae. The slightly lower figure of *Musca* larvae in Khartoum North and the abundance of the other larvae there was probably due to the permeable subsoil and higher water table in this place. There was no clear correlation between the type of superstructure and the presence of *Musca* larvae, and it has been found that *M. domestica vicina* can breed in very dark non-fly-proof latrines.

Cow manure.—House-flies seldom breed in single deposits, but very many larvae may be found in heaps of manure unless these are rendered unattractive by being turned several times.

As King (1908) pointed out, many flies breed during the preparation of *zibla.* This is a mixture of cow dung and stable refuse which is allowed to mature and is used for plastering mud buildings, particularly at the end of the rains.

Horse manure.—Horse manure, unless heaped in large quantities, tends to dry quickly. It is often mixed with bedding and so allows access to ants such as *Euponera sennaarensis* (Mayr) which will kill larvae of *Musca.*

Cotton seed.—Large areas of the Sudan are devoted to cotton-growing, and great quantities of seed are exported after the lint has been removed. If any seed becomes wet and rots it emits a strong smell and is very attractive to *Musca* which breeds in it readily. During the War, many thousands of tons of seed accumulated and much was buried in large pits and covered with earth. Some was used as fuel for railway and other engines and on occasions produced great numbers of flies. Larvae and puparia were sometimes found in the few seeds which had fallen on the foot-plates of railway engines. Flies can breed in cotton seed used as manure. Usually, however, the seed is not allowed to accumulate since it harbours pests of cotton.

The species of Musca *in the Sudan.*

Thirteen species and one subspecies of *Musca* are found in the Sudan. *M. nebulo* F. was once reported to be widely distributed in the Sudan by Patton but the species in question was possibly *M. cuthbertsoni* Patt. (Patton, 1936, p. 472). *M. vitripennis* Mg. was recorded from the Sudan by Patton (1933) but has not been found since and is meanwhile omitted from the Sudan list. *M. conducens* Wlk., *M. fasciata* Stein, *M. tempestatum* (Bezzi), *M. tempestiva* Fall., *M. crassirostris* Stein and *M. autumnalis* Deg. are reported by West (1951) to be haematophagous, and according to Patton (1933), *M. lucidula* (Lw.) and *M. xanthomelas* Wied. feed on blood.

Musca (*Musca*) *cuthbertsoni* Patt., which Cuthbertson (1937) found to be attracted by decomposing animal matter, is known from the Bahr el Jebel km. 50, measured from the Bahr el Ghazal junction (bred from paunch contents of cow), Juba (bred from potatoes), Kadugli, Khartoum (bred from cow and horse dung), J. Mahariqat, Nukheila, Port Sudan, Singa, " Sudan " (van Emden, 1941*a*), Tageru, Tonj (bred from paunch contents of cow) and Wad Medani (bred from horse manure and contents of a latrine bucket).

M. (*M.*) *domestica* L. has been found in aircraft arriving at Khartoum (Whitfield, 1939). *M. domestica vicina* Macq., the subtropical and tropical subspecies of *M. domestica*, differs from the typical form in the shape of the head of the male which is figured by Patton (1936). The subspecies is widely distributed in the Sudan and has been recorded from Bahr es Salam area, Delami, J. Elba (R.C.M.-D.), Fangak (on ulcer on man), Gebeit, Kadugli, Kassala, Khartoum (Becker, 1923, as *M. domestica* but the specimens were probably the ssp. *vicina*), Malakal, Melut and El Obeid (Becker, 1923), Port Sudan, Sennar (Becker, 1923, as *M. domestica*), Suakin, Tokar, Wad Arud, Wadi Halfa, Wad Medani and Wau.

In the Sudan *M. domestica vicina* has been bred from human faeces, cow, donkey, rabbit and horse dung, pit and bucket latrines, paunch contents of sheep, and rotting cotton seed, melons and potatoes. In Egypt, cow dung is unattractive to this species (Hafez, 1941*a*). Larvae were found at Suakin in pit latrines made dark with well-built metal superstructures but not fly-proof. It is known that adults prefer to lay eggs in well-lit situations and it may be that the larvae had hatched from eggs laid on refuse which had fallen into the pits. The larvae were living at the edge of the pits, where sand had fallen in, and many dead larvae and puparia were floating in the central liquid part of the pit contents.

Musca (*Byomyia*) *albina albina* Wied. is an easily recognised semi-desert form (Patton, 1933) with a whitish puparium (West, 1951), which occurs at Khartoum (van Emden, 1948*b*).

M. (*B.*) *conducens* Wlk. can scratch off a scab but cannot draw blood from the intact skin (Patton, 1933). It has been found at Fangak (feeding on a cow, P.A.B.), Pachala and Port Sudan.

M. (*B.*) *fasciata* Stein has been found on a cow's ulcer at Fangak (P.A.B.) and at Pachala.

M. (*B.*) *lucidula* (Lw.), which has a metallic-green abdomen, is known from Khartoum. El Obeid (Becker, 1923), Umm Inderaba (W.R., on gazelle) and Wadi Halfa, and has been bred from cow and horse dung.

M. (*B.*) *sorbens* Wied. (of which *M. primitiva* Wlk. is a synonym according to Patton who is quoted by Aubertin, 1934) is known from Atbara (Becker, 1923, as *M. humilis*), Delami, Dilling (Becker, 1923), Dueim, J. Elba (R. C. M.-D.), Fangak (on human ulcer), El Gheibish (Becker, 1923), Hawata, Joghana (Becker, 1923), Kalokitting, Keilak, Khartoum, Kongor (on human ulcer), Kosti (Becker, 1923), Maruko (on human ulcer), Mvolo, Nagishot, Nukheila Oasis, El Obeid, Rahib wells, Saoleil, Sennar (Becker, 1923), Shendi, Suakin, Sungikai area (Becker, 1923), Tageru, Talodi and Tonga (Becker, 1923), Wadi Halfa, Wad Medani and Wau.

In Egypt, cow dung is the main breeding place of *M. sorbens* (Hafez, 1941*a*). In the Sudan it has been bred from human faeces, pit latrines and horse dung.

M. sorbens was the commonest species obtained by Whitfield (1939) in aircraft at Khartoum. The numbers of each species of *Musca* were: *M. domestica* and ssp. *vicina*, 575; *M. sorbens*, 850; *M. sorbens alba*, 7; *M. tempestiva*, 1.

As Patton (1933) remarks, *M. sorbens* often alights on human skin in search of moisture, and dwarf specimens are particularly annoying. He points out that, since this species often breeds in isolated deposits of manure and human faeces, premature pupation and consequently dwarf specimens are common.

M. (*B.*) *sorbens alba* (Mall.), considered to be a variety by van Emden (1939), was regarded by its describer as a desert form similar to the pale form of *M. domestica* from the same area, the Sudan. According to van Emden (1948*b*) it is a desert form known from the Sudan and Tunisia with transitional forms in Arabia. In the Sudan it is known from Dueim (Malloch, 1929), Elai, Kalokitting, Khartoum (Malloch, 1929), Kelling area, Nukheila, Rahib wells and Tageru.

M. (*B.*) *tempestatum* (Bezzi), a small species, is known from Buram, Fangak (feeding on cow, P.A.B.), Meshra er Req, "Sudan" (van Emden, 1941*a*) and Umm Dona.

M. (*B.*) *tempestiva* Fall. is known from Fangak, Golsa, Kassala (bred from cow dung) and Khartoum (Malloch, 1925*a*), and Becker (1923) recorded it provisionally from Sennar.

M. (*Philaematomyia*) *crassirostris* Stein, according to Patton (1933), is easily recognised by its characteristic colour and bulbous mentum, and is a voracious blood sucker, scratching and tearing the skin. It is known from Delami (biting donkey), Kassala, Khartoum (bred from cow dung), S. of Kosti, K. Lolle and Renk (Becker, 1923), Saoleil, Talodi, Tonga (Becker, 1923) and Umm Dona (biting cattle).

M. (*Eumusca*) *autumnalis* Deg., which has a whitish puparium (West, 1951), has been bred from cow manure at Kassala.

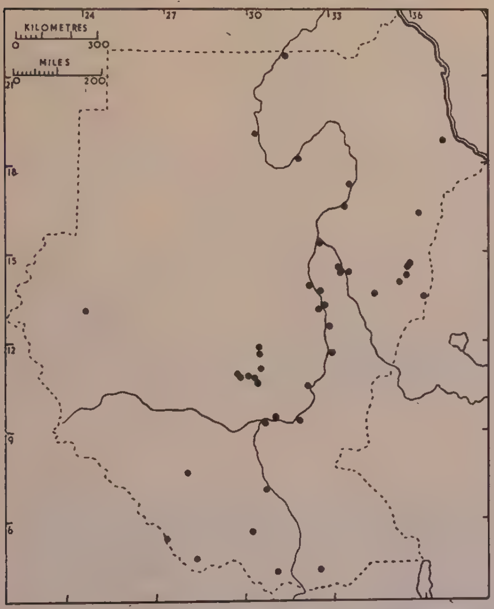
M. (*E.*) *lusoria* Wied., of which *M. alpesa* Wlk. is a synonym according to West (1951), is known from Chalamni (M.S.), Fangak (on a cow's ulcer) (determined as *M. alpesa* Wlk.), Golsa, Juba (bred from trunk of banana plant), Kassala, J. Mahariqat, Nagishot, Roseires, " Sudan " (van Emden, 1948*b*) and Wad Medani (bred from cow dung).

M. (*E.*) *xanthomelas* Wied., according to Patton (1933), who points out that it is not very easy to identify, is common in the Sudan, especially at Khartoum, and is seen only on animals and near cow dung. It is known from Buram, Fangak (on cow's ulcer), Golsa, Kassala (bred from cow dung), Khartoum, El Obeid, Pachala and Wad Medani. At Wad Medani it often breeds, with *M. domestica vicina*, in cow dung, and is readily detected by its whitish puparium.

STOMOXYDINAE.

Stomoxys.

Stomoxys brunnipes Grünb. is known from Aga Falls, Li Rangu, Li Yubu, Meridi, Shitata, " Sudan " (van Emden, 1941*a*) and Yambio. It bites man in the Sudan.



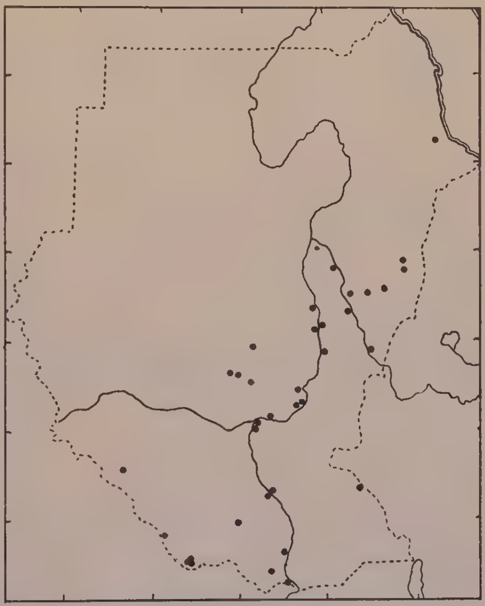


Fig. 2.—The known distribution of *Stomoxys calcitrans* in the Sudan.
Fig. 3.—The known distribution of *Stomoxys nigra* in the Sudan.

Stomoxys calcitrans (L.), which occurs throughout Europe and Asia (Bequaert, 1930), is widely distributed owing to its association with man, according to Séguy (1937). In the Sudan it is known from Aba I., Abu Usher, Agur, Amm Adam, Danagla, Delami, Deriba, Dongola, Dueim, Erkowit, Gedaref (King, 1911), Hamad en Nil, Heiban, Jebelein, Kadowa, Kadugli, Kaka, Khartoum (Austen, 1909; King, 1911), Kosti, El Lebu, Li Rangu (Sudan Medical Service Report for 1937), Li Yubu, Loka, Mafaza (King, 1911), J. Mahariqat, Malakal, Maya Sinyora, Merowe, Moqatta, Renk (Becker, 1923; King, 1911), Shambe, Shendi, Talodi, Tonga (Becker, 1923), Torit, Umm Dorein, Umm Gidad, Wad Arud, Wadi Halfa, Wau and Zeidab. Larvae have been found in decaying millet stalks and heads, decaying grass and decaying cotton bolls.

S. nigra Macq. is generally distributed in tropical Africa (Austen, 1909; Malloch, 1932), and appears to be the most widely distributed species in the region (Séguy, 1937). In the Sudan it is known from Akurwa, Bahr el Jebel km. 500, measured from the Bahr el Ghazal junction, Buffalo Cape, Deim Zubeir (Austen, 1909), Delami, Detwok (many), Erkowit, Hamra, Jebelein, Juba, Kadugli, Kajo Kaji, Kodok (numerous, Austen, 1909), Kosti, Li Rangu, Li Yubu, Loka, Mafaza (King, 1911), Matna, Maya Sinyora, Moqatta, Mvolo, Nyinyar, Nzara, Pachala, L. Pauvendal, Renk and south of it (King, 1911), Roseires, Showak, Singa, " Sudan " (van Emden, 1941*a*), Talodi, Wad Daud, Wad Nimul, Wad Medani and Yambio (P.A.B.). According to Evans-Pritchard (1940) *Stomoxys* [probably *S. nigra*] is prevalent in the Nuer district throughout the year but is particularly conspicuous in the dry season and early rains.

S. sitiens Rond. occurs at the Deriba Lakes and Erkowit, and, like the foregoing species, bites man in the Sudan.

S. varipes Bezzi, which occurs from Nyasaland and Southern Rhodesia to Eritrea (van Emden, 1941*a*), has been found at Nagishot.

In addition to the species mentioned above, *Stomoxys taeniata* Big. has been found in an aeroplane arriving at Khartoum from the north (Whitfield, 1939).

Lyperosia.

Lyperosia (*Lyperosia*) *spinigera* (Mall.) occurs in Nyasaland and Uganda (Malloch, 1932). In the Sudan it is known from a specimen collected at Meshra ez Zeraf in 1909 and recorded by King (1911) as *L. exigua* (de Meij.) an oriental species. Dr. van Emden informs me that the specimen is a pale form.

L. (*L.*) *thirouxi* (Roub.), of which Zumpt (1950) regards *L. potans* Bezzi as a synonym, occurs at Hawata, Jebelein (King, 1911), Kongor, Malakal, Meshra er Req and Shitata.

L. (*Glossinella*) *minuta* Bezzi occurs at K. Arbaat, Berber (King, 1911), Buram, Dam Gamad, Daweina, Delami, Dilling (common, Williams, 1913), Gemmeiza, Goz Khadra (W.R.), Hadaliya, Hawata, Kadugli, south of Juba (on waterbuck, H. H. King), Kassala, Khartoum (King, 1911, on donkey; Malloch, 1932), Loka, El Obeid (King, 1911), Saoleil, Shendi, Shitata, Singa, Tagoi, Talodi, Tokar, Umm Inderaba, Wad Ashana and Wad Medani. This species has been bred from cow dung at Khartoum. The adults bite man and camels and other animals. 40

Glossina.

Seven species of *Glossina* are found in the Sudan, and their distribution and importance have been described by Lewis (1949*a*, 1950). Potts (1951) alludes to the Sudan in discussing the distribution of tsetse flies, and the maps of Leeson (1953) and Potts (Directorate of Colonial Surveys, 1953) include the distribution of Sudan tsetse flies with those of Africa as a whole. General information on the history of the tsetse problem is given by Beaton (1949), Jackson & Shawki (1950, p. 216), Lewis (1949*b*) and Woodman (1949). *G. palpalis* var. *fuscipes* Newst. is the vector of human trypanosomiasis. The position regarding this disease, which affects a small proportion of the population, is discussed by Abbott (1952) and in the Sudan Medical Service annual report for 1951–1952.

PHAONIINAE.

According to van Emden (1942, 1943) some species of this subfamily breed in or frequent faeces and some occur in houses so that members of this subfamily may be of some slight importance from the hygienic point of view.

Limnophora.

Species of this genus breed in cow dung and in human faeces (Bohart & Gressitt, 1951). *Limnophora bisetosa* (Huckett) occurs at Delami, Erkowit, Khartoum, Koalib and Shambat, *L. notabilis* Stein (which is distributed over the whole Ethiopian Region according to van Emden, 1948*a*) at Khartoum, *L. obsignata* (Rond.) at Gilo (C.E.W.), *L. rufimana* (Strobl) at Khartoum, and *L. translucida* Stein (a widely distributed Ethiopian species according to van 45
Emden, 1948*a*) at Nagishot.

Dichaetomyia.

Dichaetomyia albivitta (Stein) has been found at Lotti, *D. fumaria* (Stein) at Lotti and Nagishot, *D. liberia* Curran at Meridi, and *D. pallidula* Curran at Delami and Meridi (W.R.). *D. quadrata nubiana* (Big.) is found on cow dung in Southern Rhodesia (van Emden, 1942) and will feed on human faeces (Cuthbertson, 1933, as *Mydaea lineata* (Stein)). It is known from Khartoum (van 51
Emden, 1951), Talodi and Yambio (C.E.W.). *D. serena* (Stein), a species which settles on cow dung (Cuthbertson, 1937) and frequents houses (van Emden, 1942), is known from Deriba Lakes, Kelling (van Emden, 1951) and Nagishot.

Hydrotaea.

British species of *Hydrotaea* often congregate round houses and cattle, and are attracted to human perspiration (Colyer & Hammond, 1951; Patton, 1931), and some European species feed on wounds and secretions of cattle (Hammer, 57
1941). *H. polita* Emd. (van Emden, 1943) was found on an ulcer on a man at Maruko.

Ophyra.

Ophyra capensis (Wied.), a metallic-green fly which is widely distributed in the Palaearctic and Ethiopian Regions (van Emden, 1948*b*), has been taken in 53
a fly trap at Khartoum.

Dimorphia.

Dimorphia tristis (Wied.), which probably occurs in the whole Ethiopian
Region (van Emden, 1948*a*) and has been found on faeces in Southern Rhodesia 4
(Cuthbertson, 1933), occurs at Lotti and Nagishot.

Phaonia.

Phaonia abnormis (Stein), which is known to settle on human faeces (Cuthbertson, 1937) and to frequent houses (van Emden, 1943), occurs at Delami, 55
Erkowit, Nagishot and Umm Dona.

Gymnodia.

Gymnodia flavescens (Stein), which was originally described from Egyptian
material (Curran, 1937), has been bred from cow dung at Wad Medani, and 7
G. mervinia (Wlk.) has been found at Nagishot.

Mydaea.

Larvae of *Mydaea* have mouth parts of a carnivorous type (Muirhead Thomson, 1947). *M. geniculata* Stein, which occurs from the Sudan to Southern
Rhodesia (van Emden, 1948*a*), is found at Nagishot (van Emden, 1951), and 31
M. (*Myiospila*) *maculinervis* (Mall.) also occurs there.

Pyrellina.

Species of *Pyrellina*, which is an exclusively Ethiopian genus (Séguy, 1937), have been found on dung in Southern Rhodesia by Cuthbertson (1933). *P. distincta* (Wlk.) is known from Lotti and Nagishot, a variety of *P. inventrix* (Wlk.) from Lotti, and *P. ruficauda* Mall. from Nagishot.

LISPINAE.

The adults of this subfamily prey largely on different stages of mosquitos (van Emden, 1941*b*). Six species, all of one genus, are known in the Sudan.

Lispe.

Lispe bivittata Stein is known from Roseires, *L. leucospila* (Wied.) from Khartoum and Shendi (A.H.H.), *L. modesta* Stein from Tub el Hagur, *L. nivalis* Wied. from Khartoum and Roseires, *L. nuba* Wied. from Manaqil, and *L. pygmaea* Fall. from Khartoum and Shambat.

COENOSIINAE.

This subfamily is very richly developed in the Ethiopian Region (van Emden, 1941*a*).

Atherigona.

Some species of *Atherigona* (*viz.*, the subgenus *Acritochaeta*, *sensu lato*) feed in the larval stage on decaying vegetables and fruits, and others on living plants, according to Malloch (1925*b*). Of the Sudan species mentioned below he records *A. excisa* (Thoms.) and *A. nudiseta* Mall. from India and points out that the former is probably distributed by commerce in the warmer parts of the world. The larvae of most of the other Indian species feed on living plants. The adults of *A. excisa* feed on human wounds in Samoa (Satchell & Harrison, 1953).

A. aberrans Mall. has been bred from horse dung at Khartoum (R.C.). *A. bedfordi* Emd. occurs at Khartoum, Shambat and Shendi (bred from millet, van Emden, 1940) and *A. budongoana* Emd. at Nagishot. *A.* (*Acritochaeta*) *excisa* (Thoms.) is known from Geili, Juba, Kagelu, Kamlin, Khartoum, Shambat, Shendi, Soba and Wad Medani, and has been bred from cotton bolls, grapefruit, millet stalks and potatoes, all in a decayed condition. According to Cuthbertson (1932, 1936) this species is widely distributed in Africa and the East, and breeds in cow dung where its carnivorous larvae feed on those of *Musca* and other genera. *A. excisa* is considered to be a vector of " filth-diseases " in Guam by Bohart & Gressitt (1951). *A. ferruginea* Emd. occurs at Shambat (van Emden, 1940), and *A. griseiventris* Emd. has been caught in a fly trap at Wau. *A. haplopyga* Emd. has been found at Lotti (van Emden, 1940) and *A. nudiseta* Mall. at Gureir and Shambat, *A. steeleae* Emd. (a species known from Ethiopia and Uganda, van Emden, 1941*a*) at Shendi (bred from millet, van Emden, 1940) and Lotti, and *A. trapezia* Emd. (which occurs from Southern Rhodesia to the Sudan, van Emden, 1941*a*) at Lotti.

FANNIINAE.

Fannia.

Fannia suturalis Stein occurs at Nagishot, and *F. canicularis* (L.) has been found at Khartoum in at aeroplane from Durban (Whitfield, 1939).

Summary.

The general distribution of the MUSCIDAE (other than *Glossina*) of medical interest in the Sudan is discussed, and brief notes are given on some Muscids in relation to trypanosomiasis.

Eighty-six species of some medical interest, belonging to 22 genera, are listed, with records of their distribution and notes on the habits of several of them.

Acknowledgements.

I am indebted to the Commonwealth Institute of Entomology for the identification of many species; to Dr. F. I. van Emden for numerous identifications and advice on many points; Mr. F. W. Blake, Dr. J. F. E. Bloss (Pachala), Mr. W. Bushe (Tageru), Professor P. A. Buxton, C.M.G., F.R.S. (flies on ulcers), Mr. R. Cottam, Khidr Eff. Ahmed Abdel Hai, the late Abdullah Eff. Hussein, the late Mr. H. H. King, Mr. R. C. Maxwell-Darling, Mr. H. J. Morris, Mr. W. Ruttledge, Mohammed Eff. Shaar (Wau), Miss M. Steele (Deriba Lakes, Isoke and Lotti), Mr. J. K. M. Trew (Nukheila and Rahib wells) and Mr. C. E. Wilson for contributing specimens from the places indicated above or shown in the text.

References.

ABBOTT, P. H. (1952). Observations on the control of sleeping sickness among the Azande of the southern Sudan.—E. Afr. med. J., **29**, pp. 297–309.

AUBERTIN, D. (1934). Report on the Insecta collected by Colonel R. Meinertzhagen in the Ahaggar Mountains. VI. Diptera.—Ann. Mag. nat. Hist., (10) **13**, pp. 186–188.

AUSTEN, E. E. (1909). Illustrations of African blood-sucking flies other than mosquitoes and tsetse-flies.—221 pp., London, Brit. Mus. (Nat. Hist.).

BALFOUR, A. (1906). Biting and noxious insects other than mosquitoes.—2nd Rep. Wellcome trop. Res. Lab., pp. 29–50.

BEATON, A. C. (1949). Equatoria Province handbook, **2.** Khartoum.

BECKER, T. (1923). Wissenschaftliche Ergebnisse der von Werner unternommenen zoologischen Expedition nach dem Anglo-Aegyptischen Sudan (Kordofan) 1914. VI. Diptera.—Denkschr. Akad. Wiss. Wien., **98**, pp. 57–82.

BEQUAERT, J. (1930). Medical and economic entomology.—*In* Strong, R. P. *Ed.* The African Republic of Liberia and the Belgian Congo, **2**, pp. 797–1001, Cambridge, Mass., Harvard Univ. Pr.

BOHART, G. E. & GRESSITT, J. L. (1951). Filth-inhabiting flies of Guam.—Bull. Bishop Mus., no. 204, 152 pp.

BUXTON, P. A. (1949). Notes on trypanosomiasis and tsetse in the southern parts of the Anglo-Egyptian Sudan.—Bur. perm. interafr. Tsé-tsé Tryp., no. 85, 11 pp., multigraph.

COLYER, C. N. & HAMMOND, C. O. (1951). Flies of the British Isles.—383 pp. London, Warne.

CURRAN, C. H. (1937). African Muscidae. IV (Diptera).—Amer. Mus. Novit., no. 931, 14 pp.

CUTHBERTSON, A. (1932). Notes on the habits of some Diptera in Rhodesia.—Proc. Rhod. sci. Ass., **31**, pp. 31–36.

CUTHBERTSON, A. (1933). The habits and life histories of some Diptera in Southern Rhodesia.—Proc. Rhod. sci. Ass., **32**, pp. 81–111.

CUTHBERTSON, A. (1934). Biological notes on some Diptera in Southern Rhodesia.—Proc. Rhod. sci. Ass., **33**, pp. 32–50.

CUTHBERTSON, A. (1936). Biological notes on some Diptera of Southern Rhodesia.—Occ. Pap. Rhod. Mus., no. 5, pp. 46–63.

Cuthbertson, A. (1937). Biological notes on some Diptera in Southern Rhodesia.—Proc. Rhod. sci. Ass., **35,** pp. 16–34.

Directorate of Colonial Surveys. (1953). Distribution of tsetse species in Africa. Sheet 2 [map, 1:5,000,000].—D.C.S. (Misc.) 48b.

van Emden, F. (1939). Muscidae: Muscinae and Stomoxydinae.—Ruwenzori Exped. 1934–5, **2,** pp. 49–89. London, Brit. Mus. (Nat. Hist.).

van Emden, F. I. (1940). Muscidae: B. Coenosiinae.—Ruwenzori Exped. 1934–5, **2,** pp. 91–255. London, Brit. Mus. (Nat. Hist.).

van Emden, F. I. (1941*a*). Entomological expedition to Abyssinia, 1926–27. Diptera Cyclorrhapha: Muscidae, I.—Ann. Mag. nat. Hist., (11) **8,** pp. 210–234.

van Emden, F. I. (1941*b*). Keys to the Muscidae of the Ethiopian Region: Scatophaginae, Anthomyiinae, Lispinae, Faniinae.—Bull. ent. Res., **32,** pp. 251–275.

van Emden, F. I. (1942). Keys to the Muscidae of the Ethiopian Region: *Dichaetomyia*-group.—Ann. Mag. nat. Hist., (11) **9,** pp. 673–701, 721–736.

van Emden, F. I. (1943). Keys to the Muscidae of the Ethiopian Region: *Phaonia*-group.—Ann. Mag. nat. Hist., (11) **10,** pp. 73–101.

van Emden, F. I. (1948*a*). Entomological expedition to Abyssinia, 1926–27. Diptera Cyclorrhapha: Muscidae, II.—Ann. Mag. nat. Hist., (11) **14,** pp. 460–484.

van Emden, F. I. (1948*b*). Diptera: Muscidae.—Exped. S.-W. Arabia 1937–8, **1,** pp. 161–175. London, Brit. Mus. (Nat. Hist.).

van Emden, F. I. (1951). Muscidae: C. Scatophaginae, Anthomyiinae, Lispinae, Fanniinae and Phaoniinae.—Ruwenzori Exped. 1934–5, **2,** pp. 325–710. London, Brit. Mus. (Nat. Hist.).

Evans-Pritchard, E. E. (1940). The Nuer: a description of the modes of livelihood and political institutions of a Nilotic people. Oxford.

Hafez, M. (1941*a*). Investigations into the problem of fly control in Egypt.—Bull. Soc. Fouad Ier Ent., **25,** pp. 99–144.

Hafez, M. (1941*b*). A study of the biology of the Egyptian common house-fly *Musca vicina* Macq. (Diptera: Muscidae).—Bull. Soc. Fouad Ier Ent., **25,** pp. 163–189.

Hammer, O. (1941). Biological and ecological investigations on flies associated with pasturing cattle and their excrement.—Vidensk. Medd. Dansk naturh. Foren., **105,** 257 pp.

Jackson, J. K. & Shawki, M. K. (1950). Shifting cultivation in the Sudan with particular reference to forestry.—Sudan Notes, **31,** pp. 210–222.

King, H. H. (1908). Report on economic entomology.—3rd Rep. Wellcome trop. Res. Lab., pp. 201–248.

King, H. H. (1911). Report of the Entomological Section. . . .—4th Rep. Wellcome trop. Res. Lab., B, pp. 95–150.

Leeson, H. S. (1953). The recorded distribution of certain tsetse flies and of human trypanosomiasis in Africa.—Trans. R. Soc. trop. Med. Hyg., **47,** pp. 130–133.

Lewis, D. J. (1949*a*). The tsetse fly problem in the Anglo-Egyptian Sudan.—Sudan Notes, **30,** pp. 179–210.

LEWIS, D. J. (1949*b*). *In* Beaton, A. C. Equatoria Province handbook, **2,** pp. 162–167. Khartoum.

LEWIS, D. J. (1950). Notes on tsetse flies in the Anglo-Egyptian Sudan.—Sudan Notes, **32,** pp. 96–105.

LEWIS, D. J. (1953). The Tabanidae of the Anglo-Egyptian Sudan.—Bull. ent. Res., **44,** pp. 175–216.

MALLOCH, J. R. (1925*a*). Exotic Muscaridae (Diptera). XVII.—Ann. Mag. nat. Hist., (9) **16,** pp. 361–377.

MALLOCH, J. R. (1925*b*). Some Indian species of the Dipterous genus *Atherigona*, Rondani.—Mem. Dep. Agric. India (Ent. Ser.), **8,** pp. 111–125.

MALLOCH, J. R. (1929). Exotic Muscaridae (Diptera). XXIV.—Ann. Mag. nat. Hist., (10) **3,** pp. 249–280.

MALLOCH, J. R. (1932). Exotic Muscaridae (Diptera). XXXVI.—Ann. Mag. nat. Hist., (10) **9,** pp. 377–405, 421–447, 501–518.

MUIRHEAD THOMSON, R. C. (1947). Notes on the breeding habits and early stages of some Muscids associated with cattle in Assam.—Proc. R. ent. Soc. Lond., (A) **22,** pp. 89–100.

PATTON, W. S. (1931). Insects, ticks, mites and venomous animals of medical and veterinary importance. Part II. Public health.—740 pp. Liverpool.

PATTON, W. S. (1932). Studies on the higher Diptera of medical and veterinary importance. A revision of the species of the genus *Musca* based on a comparative study of the male terminalia. I. The natural grouping of the species. . . .—Ann. trop. Med. Parasit., **26,** pp. 347–405.

PATTON, W. S. (1933). Studies on the higher Diptera . . . [on *Musca* and (the last section) *Stomoxys*].—Ann. trop. Med. Parasit., **27,** pp. 135–156, 327–345, 397–430, 501–537.

PATTON, W. S. (1936). Studies on the higher Diptera . . . [the Ethiopian species of *Musca*].—Ann. trop. Med. Parasit., **30,** pp. 469–490.

PATTON, W. S. & GIBBINS, E. G. (1934). Studies on the higher Diptera . . . The metallic Muscini.—Ann. trop. Med. Parasit., **28,** pp. 571–578.

POTTS, W. H. (1951). The distribution of tsetse flies in Africa.—Bur. perm. interafr. Tsé-tsé Tryp., no. 157/0, multigraph.

SATCHELL, G. H. & HARRISON, R. A. (1953). Experimental observations on the possibility of transmission of yaws by wound-feeding Diptera, in western Samoa.—Trans. R. Soc. trop. Med. Hyg., **47,** pp. 148–153.

SÉGUY, E. (1937). Diptera Fam. Muscidae.—Genera Insect., **205,** 595 pp.

SÉGUY, E. (1950). La biologie des Diptères.—Encycl. ent., (A) **26,** 609 pp.

SUDAN MEDICAL SERVICE. (1938–52). Annual reports for the years 1937 to 1952. Khartoum.

WEST, L. S. (1951). The housefly: its natural history, medical importance and control.—584 pp. Ithaca, N.Y., Comstock; London, Constable.

WHITFIELD, F. G. S. (1939). Air transport, insects and disease.—Bull. ent. Res., **30,** pp. 365–442.

WILLIAMS, A. J. (1913). Notes on an outbreak of horse-sickness connected with the presence of a *Lyperosia* as possible transmitter.—Vet. J., **69,** pp. 382–386.

WOODMAN, H. M. (1949). Medical. *In* Beaton, A. C. Equatoria Province handbook, **2,** pp. 71–93. Khartoum.

ZUMPT, F. (1950). 5th preliminary study to a monograph of the Stomoxydinae. Key to the Stomoxydinae of the Ethiopian Region, with description of a new *Haematobia* and a new *Rhinomusca* species from Zululand.—An. Inst. Med. trop., **7**, pp. 397–426.

ZUMPT, F. (1951). Myiasis in man and animals in Africa.—S. Afr. J. clin. Sci., **2**, pp. 38–69.

OBSERVATIONS ON THE INCIDENCE OF TRYPANOSOMES IN *GLOSSINA PALPALIS* (R.-D.) IN SIERRA LEONE.

By F. A. Squire.
Director, Department of Tsetse Control, Gold Coast.

M A.W

As shown previously (Squire, 1951), there is a marked seasonal variation in the incidence of *Trypanosoma vivax* in *Glossina palpalis* (R.-D.). The results of further dissections from September 1949 to November 1951 are given in Table I. At the same time the opportunity is taken of repeating data already

TABLE I.

Incidence of *T. vivax* in *G. palpalis*, September 1948 to November 1951, showing number of flies dissected, number found infected with *T. vivax* (in parenthesis) and percentage infected.

Month	Age-group 2				Age-group 3			
	Males		Females		Males		Females	
1948 Sept. ..	129(17)	13·2	47 (4)	8·5	36 (4)	11·1	12 (3)	25·0
Oct. ..	45 (2)	4·4	25 (3)	12·0	23 (4)	17·4	7 (2)	28·6
Nov. ..	112 (2)	1·8	46 (0)	0·0	55 (2)	3·6	23 (2)	8·7
Dec. ..	157 (2)	1·3	18 (0)	0·0	58 (3)	5·2	15 (1)	6·7
1949 Jan. ..	81 (0)	0·0	9 (0)	0·0	46 (0)	0·0	9 (1)	11·2
Feb. ..	34 (1)	2·9	5 (0)	0·0	13 (0)	0·0	3 (1)	33·3
Mar. ..	160 (5)	3·1	16 (0)	0·0	52 (2)	3·8	17 (1)	5·9
Apr. ..	54 (2)	3·7	6 (0)	0·0	33 (3)	9·1	7 (1)	14·3
May ..	49 (2)	4·1	3 (0)	0·0	32 (2)	6·3	8 (0)	0·0
June ..	84 (2)	2·4	38 (1)	2·6	28 (4)	14·3	16 (3)	18·8
July ..	142 (8)	5·6	63 (6)	9·5	39 (3)	7·7	37 (8)	21·6
Aug. ..	173 (9)	5·2	83 (9)	10·8	37 (4)	10·8	28 (4)	14·3
Totals (Sept. 1948–Aug. 1949) ..	1,220(52)	4·3	359(23)	6·4	452(31)	6·8	182(27)	14·3
1949 Sept. ..	204(12)	5·9	42 (4)	9·5	50 (0)	0·0	21 (2)	9·5
Oct. ..	100 (9)	9·0	38 (3)	7·9	10 (1)	10·0	7 (3)	42·9
Nov. ..	124 (6)	4·8	52 (2)	3·8	33 (2)	6·1	4 (0)	0·0
1950 Feb. ..	114 (3)	2·6	34 (0)	0·0	15 (1)	6·7	5 (0)	0·0
Mar. ..	299 (4)	1·3	27 (0)	0·0	35 (2)	5·7	9 (0)	0·0
Apr. ..	136 (0)	0·0	10 (1)	10·0	16 (1)	6·3	4 (0)	0·0
June ..	83 (1)	1·2	2 (0)	0·0	6 (0)	0·0	– –	–
July ..	223 (8)	3·6	1 (0)	0·0	42 (4)	9·5	3 (1)	33·3
Aug. ..	192 (9)	4·6	– –	–	29 (4)	13·8	– –	–
Sept. ..	174 (7)	4·0	22 (3)	13·7	25 (4)	16·0	8 (1)	12·5
Oct. ..	188 (3)	1·6	– –	–	33 (5)	15·2	– –	–
Nov. ..	39 (0)	0·0	– –	–	3 (0)	0·0	– –	–
Dec. ..	– –	–	– –	–	85 (6)	7·1	18 (2)	11·1
1951 Jan. ..	– –	–	– –	–	32 (4)	12·5	8 (0)	0·0
Feb. ..	– –	–	– –	–	62 (2)	3·2	20 (0)	0·0
Mar. ..	150 (2)	1·3	9 (0)	0·0	62 (2)	3·2	7 (0)	0·0
Apr. ..	184 (4)	2·2	12 (1)	8·4	58 (0)	0·0	13 (3)	23·1
May ..	106 (0)	0·0	4 (0)	0·0	17 (0)	0·0	2 (0)	0·0
June ..	122 (3)	2·5	– –	–	6 (1)	16·7	– –	–
July ..	68 (4)	5·9	– –	–	9 (0)	0·0	– –	–
Aug. ..	84 (6)	7·1	– –	–	7 (0)	0·0	– –	–
Sept. ..	46 (4)	8·7	– –	–	3 (0)	0·0	– –	–
Oct. ..	77 (4)	5·2	– –	–	13 (2)	15·5	– –	–
Nov. ..	83 (4)	4·8	13 (0)	0·0	36 (3)	8·4	4 (0)	0·0
Totals (Sept. 1949–Nov. 1951) ..	2,796(93)	3·3	266(14)	5·3	687(44)	6·4	133(12)	9·0

published in the paper referred to above but now showing the incidence of infection separately in the two sexes from September 1948 to August 1949.

The specific diagnosis of the trypanosomes is based on their position in the fly: thus trypanosomes found in the proboscis only are called *T. vivax*; those found in the proboscis and the mid-gut, or only in the mid-gut, *T. congolense*, despite the possibility of double infections with *T. vivax* and *T. congolense*. The incidence shown of *T. vivax* may therefore err on the conservative side. No cases with infected labial glands were seen. Age-group 1 has been omitted from Table I owing to its low rate of infection: from September 1949 onwards this age-group was not dissected.

It will be seen that the new data lend support to the argument of seasonal variation in the incidence of *T. vivax*, the highest rates of infection being recorded during the months of heavy rain. The data on this point for flies of age-group 2 are summarised in Table III and illustrated in fig. 1. There is an inverse correlation between the mean daily sunshine and the incidence of infection. The coefficient of correlation between monthly means of infection rate and of hours of sunshine, calculated from the data of Table III is $-0{\cdot}49$, which is significant ($P < 0{\cdot}05$).

TABLE II.

Incidence of *T. congolense* in *G. palpalis*, November 1948 to November 1950, showing number of flies dissected and number infected (in parenthesis).

Month	Age-group 2		Age-group 3	
	Male	Female	Male	Female
1948 November	112 (0)	46 (0)	55 (1)	23 (1)
December	157 (0)	18 (0)	58 (0)	15 (0)
1949 January	81 (0)	9 (0)	46 (0)	9 (0)
February	34 (0)	5 (0)	13 (0)	3 (0)
March	160 (0)	16 (0)	52 (0)	17 (0)
April	54 (1)	6 (1)	33 (2)	7 (0)
May	49 (0)	3 (0)	32 (4)	8 (0)
June	84 (0)	38 (0)	28 (1)	16 (0)
July	142 (0)	63 (0)	39 (0)	37 (0)
August	173 (4)	83 (0)	37 (3)	28 (3)
September	204 (3)	42 (0)	50 (0)	21 (0)
October	100 (1)	38 (0)	10 (0)	7 (1)
November	124 (1)	52 (0)	33 (2)	4 (0)
1950 February	114 (0)	34 (0)	15 (0)	5 (0)
March	299 (0)	27 (0)	35 (0)	9 (0)
April	136 (0)	10 (0)	16 (0)	4 (0)
June	83 (0)	2 (0)	6 (0)	–
July	223 (0)	1 (0)	42 (0)	3 (0)
August	192 (1)	–	29 (0)	–
September	174 (7)	22 (0)	25 (0)	8 (0)
October	188 (0)	–	33 (0)	–
November	39 (0)	–	3 (0)	–
December	–	–	85 (1)	18 (0)
1951 January	–	–	32 (0)	8 (0)
February	–	–	62 (1)	20 (0)
March	150 (0)	9 (0)	62 (1)	7 (0)
April	184 (1)	12 (0)	58 (1)	13 (0)
May	106 (2)	4 (0)	17 (0)	2 (0)
June	122 (2)	–	6 (0)	–
July	68 (0)	–	9 (1)	–
August	84 (1)	–	7 (1)	–
September	46 (0)	–	3 (0)	–
October	77 (0)	–	13 (0)	–
November	83 (1)	13 (1)	36 (1)	4 (0)
Totals	3,842(25)	553 (2)	1,080(20)	296 (5)
Percentage infected	0·7	0·4	1·9	1·7

The practical importance of this seasonal fluctuation in the incidence of infection is obvious. Its cause is obscure. Nash & Page (1953) adhere to the old belief that it is simply due to the rising average age of the population during the wet season, which they attribute not to the cessation of emergences but to the increased longevity of the fly at the beginning of and during the rains. They do not appear to appreciate the absolute nature of the evidence yielded by the process of age-grouping. Thus AG.2 represents an age-group which does not vary (except in size) with the average age of the population. Moreover, there is no evidence of increased longevity at the beginning of and during the rains in Sierra Leone, though there is in the more extreme climate of northern Nigeria. There remains the question of the seasonal variability of the age-groups. It is possible that flies wear out their wings more rapidly in the hot season, thus appearing older than they are (Jackson, 1946). This is admittedly an unknown factor which has not been taken into account, though here again it is likely to be less marked in Sierra Leone than in northern Nigeria. Jackson (1948), working on *G. swynnertoni* Aust. and *G. morsitans* Westw. in Tanganyika, concluded tentatively that there was no indication of any difference in the rate of fray in the wet and dry seasons.

TABLE III.

Mean daily hours of sunshine and incidence of infection with *T. vivax* in *G. palpalis* males and females of age-group 2.

Month	Mean daily sunshine				Rate of infection			
	1949	1950	1951	Mean	1949	1950	1951	Mean
February		8·4		8·4		2·0		2·0
March		6·8	8·6	7·7		1·2	1·3	1·3
April		5·3	7·7	6·5		0·7	2·5	1·6
May			5·2	5·2		0·0		0·0
June		6·8	5·2	6·0		1·2	2·4	1·8
July		3·0	2·3	2·7		3·6	5·8	4·7
August		2·5	2·0	2·3		4·7	7·1	5·9
September	5·0	2·5	4·4	4·0	6·5	5·1	8·7	6·8
October	6·2	6·0	4·4	5·5	8·7	1·6	5·2	5·2
November	6·4		6·5	6·5	4·5		4·2	4·4

It should be stressed that it is not suggested that the amount of sunshine *per se* is necessarily the determining factor or that there is necessarily any direct causal relationship between seasonal weather conditions as a whole and the incidence of infection. The phenomenon may be due to some indirect or even extraneous cause. It is, however, worth noting that *T. congolense* (Table II) does not appear to follow this seasonal pattern. This trypanosome is ecologically much more sheltered for part of its life-cycle in the fly than *T. vivax*, which occurs only in the proboscis.

Table I shows that flies in AG.3 are more heavily infected than those in AG.2. Thus in the period September 1948 to August 1949 the males are 1·5 times and the females 2·2 times as heavily infected in AG.3 as in AG.2. In the period September 1949 to November 1951 the corresponding figures are 1·9 and 1·7. In the case of *T. congolense* (Table II) the corresponding figures are even greater, *viz.*:—2·7 and 4·3. From this it is concluded that flies are infectible at all ages with both *T. vivax* and *T. congolense*. The idea that flies are only infectible when they are very young is thus not supported. Indeed the virtual absence of infection in AG.1 almost totally disproves this idea.

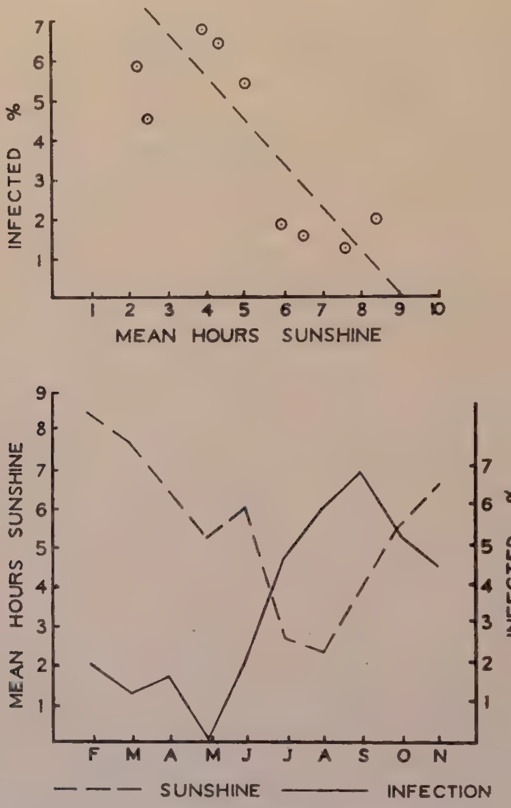


Fig. 1.—(Above): Correlation between monthly means of rate of infection of *G. palpalis* with *T. vivax* and daily sunshine.
(Below): Seasonal variation in daily sunshine and rate of infection.

The same Tables show that females are more heavily infected than males in the case of *T. vivax* but not in the case of *T. congolense*. This difference could be explained on the grounds that the female, being generally pregnant, needs and takes bigger and (or) more frequent meals than the male. Another explanation is that males by their greater activity acquire older looking wings earlier in life than the females, so that the males in any age-group may in fact be younger than the females. Jackson's (1948) findings appear to support this theory. Bulking the whole data in Table I the rate of infection of females is 1·6 times that of males in AG.2 and 1·9 times that of males in AG.3. These differences are highly significant when contingency tests are applied ($\chi^2 = 7{\cdot}7$ for age-group 2 and 11·5 for age-group 3, giving in both cases $P < 0{\cdot}01$). In the case of *T. congolense* the difference is not significant.

Attention is drawn to the fact that none of the flies dissected had infected labial glands. It thus appears that the more specialised the trypanosome the lower is its incidence in flies of a comparable age.

Summary.

Observations were made in Sierra Leone from September 1949 to November 1951 on the incidence of trypanosomes in *Glossina palpalis* (R.-D.), in continuation of those previously reported that began in September 1948. Flies were dissected; trypanosomes found to be restricted to the proboscis were classed as *Trypanosoma vivax* and those found also or only in the mid-gut as *T. congolense*. None of the flies had infected labial glands. The whole data are presented for the sexes separately by months.

The existence of a marked seasonal variation in the incidence of *T. vivax* in *G. palpalis* is confirmed. The highest rates of infection occurred in the months of heavy rain, and there was a significant inverse correlation between the monthly means of infection rate and of hours of sunshine. The cause is unknown, but possible explanations are discussed.

The older the fly, as judged by its appearance, the greater the rate of infection by both species of trypanosome; the virtual absence of infection in the youngest group of flies does not support the theory that they can only be infected when very young.

In the case of *T. vivax*, but not in that of *T. congolense*, female flies were more heavily infected than males. This may be due to a larger food intake by the females, or to males, because of their more active life, appearing to be older than they are.

Acknowledgements.

Thanks are due to Mr. W. L. Booker, Assistant Statistician of the Government Statistician's Office, Accra, for his help in the statistical analysis of the data.

References.

JACKSON, C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera).—Bull. ent. Res., **37**, pp. 291–299.

JACKSON, C. H. N. (1948). Some further isolated generations of tsetse flies.—Bull. ent. Res., **39**, pp. 441–451.

NASH, T. A. M. & PAGE, W. A. (1953). The ecology of *Glossina palpalis* in Northern Nigeria.—Trans. R. ent. Soc. Lond., **104**, pp. 71–169.

SQUIRE, F. A. (1951). Seasonal variation in the incidence of *Trypanosoma vivax* in *Glossina palpalis* (R.-D.).—Bull. ent. Res., **42**, pp. 371–374.

GENERAL INDEX.

A.

abdominale, Dactylosternum.
aberrans, Atherigona.
Abies alba, relation of *Adelges piceae* and its predators to, **252**, **255**, **261**, **272**.
abietis, Scymnus.
abnormis, Phaonia.
abyssinica, Morellia (see *M. prolectata*).
Acacia arabica, Apomecyna binubila on, **560**.
Acritochaeta (see *Atherigona*).
Acropyga paramaribensis, **105**.
aculeatus, Macromischoides.
acuminatus, Coccus.
Adelges nordmannianae (*nüsslini*), **252**.
Adelges piceae, predators of, **243–278**.
Adelgimyza, **772**.
adonidum, Pseudococcus.
Aëdes, **438**; responses of species of, to coloured cloths, **67–78**.
Aëdes aegypti, **199**, **238**, **286**, **287**, **424**, **425**, **468**, **470**, **471**, **480**; effect of atmospheric pressure on flight responses of, **507–526**.
Aëdes africanus, **199–242**.
Aëdes alternans, **286**.
Aëdes apicoargenteus, **199**, **202**, **214**.
Aëdes berlandi, **475–477**.
Aëdes cantans, **469**, **470**, **471**, **480**.
Aëdes caspius, **444**, **468**, **469**, **470**, **472**, **477**.
Aëdes cinereus, **468**, **469**, **470**, **472**, **473**.
Aëdes communis, **67**, **469**, **470**, **473**.
Aëdes dendrophilus, **199**, **214**.
Aëdes detritus, **444**, **468–473**.
Aëdes echinus, **444**, **474**.
Aëdes fitchi, **67**.
Aëdes geniculatus, **444**, **468**, **469**, **470**, **473**, **474**, **478**.
Aëdes ingrami, **199**, **230**, **231**.
Aëdes irritans, **200**.
Aëdes kermorganti, **286**.
Aëdes lepidonotus, **480**.
Aëdes longipalpis, **199**, **214**, **234–237**.
Aëdes longitubus, **468**, **469**, **470**, **472**, **475–478**.
Aëdes mariae, **444**, **468**, **469**, **470**, **472**, **477**.
Aëdes nigerrimus, **199**, **233**, **234**, **235**.
Aëdes notoscriptus, **286**, **287**.
Aëdes pembaensis, **200**, **227**.
Aëdes pionips, **67**.
Aëdes polynesiensis, **423–427**.
Aëdes praeteritus, **475**.
Aëdes pseudorusticus, **480**.
Aëdes pseudoscutellaris, **423**.
Aëdes pulchritarsis, members of complex of, **475–477**.
Aëdes pulchritarsis asiaticus, **475**.
Aëdes pulchritarsis stegomyina, **475**, **476**.
Aëdes punctor, **67**, **77**, **473**.
Aëdes quasirusticus, **480**.
Aëdes refiki, **480**.
Aëdes rusticus, **444**, **445**, **468**, **469**, **470**, **473**, **479**.
Aëdes ruwenzori, **199**, **233**.
Aëdes simici, **475**, **477**.
Aëdes simpsoni, **199**, **202**, **214**, **222**, **227**, **238**, **239**.
Aëdes stampari, **480**.
Aëdes taeniorhynchus, studies on, in Florida, **757–768**.
Aëdes vexans, **286**, **287**, **291**, **424**, **425**, **468–471**, **480**.
Aëdes vigilax, **286**, **287**, **290**, **291**.
Aëdes vittatus, **468**, **470**, **480**.
Aëdimorphus (see *Aëdes*).
Aëdomyia africana, **199**.
aegypti, Aëdes (*Stegomyia*).
Aerosols, aircraft applications of insecticides as, **79–92**, **585–603**, **605–612**, **613–622**, **745–749**.
africana, Aëdomyia; Crematogaster (*Atopogyne*); *Mansonia* (*Taeniorhynchus, Mansonioides*).
africanum, Melittomma.
africanus, Aëdes (*Stegomyia*); *Coccus; Hylecoetus* (see *Melittomma*).
agilis, Endopsylla.
Agrocide Products, **47**, **49**, **50**, **297**.
Agrotis segetum, cold-hardiness of larvae of, **335**, **336**.
Aircraft, applications of insecticides from, **79–92**, **177**, **585–603**, **605–612**, **613–622**, **745–749**.
Aitutaki (see Cook Islands).
Alaus mahenus, **44**.
alba, Musca (*Byomyia*) *sorbens.*
albigena, Orthellia.
albina, Musca (*Byomyia*).
albitarsis, Melittomma.
albivitta, Dichaetomyia.

Albizzia, Xyleborus perforans on, **43.**
Aldrex, **47, 49–53, 55, 57, 58, 709.**
Aldrin, **47, 49–53, 55, 57, 58, 137–139, 709.**
algeriensis, Anopheles.
Alluaudinella arguta, **785.**
Alluaudinella flaviceps, **785.**
Almond, Aphids on, in Israel, **623, 626–631, 634, 636.**
alpesa, Musca (see *M. lusoria*).
alternans, Aëdes (*Mucidus*).
amphibia, Dixa.
Amphipyra pyramidea, **335.**
amygdalinus, Brachycaudus.
anacardii, Helopeltis.
Anacardium occidentale (see Cashew).
Anaclysta eremophila, **785.**
Anatis ocellata, **246.**
Aneityum (see New Hebrides).
Anisopteromalus calandrae, **304, 306.**
annulata, Culiseta.
annulatus, Diplazon.
annulirostris, Culex.
Anomma nigricans (see *Dorylus*).
anonae, Stictococcus.
Anopheles, not present in New Caledonia and Belep Is., **285.**
Anopheles algeriensis, **446, 447, 449, 450, 456.**
Anopheles claviger, **444, 446, 447, 449–451, 454–457.**
Anopheles claviger petragnani, **451.**
Anopheles coustani, **367, 370.**
Anopheles coustani tenebrosus, **370.**
Anopheles coustani ziemanni, **199, 210, 211, 212.**
Anopheles demeilloni, **363.**
Anopheles farauti, and malaria in New Hebrides, **279–283, 290.**
Anopheles funestus, adult habits of, in Tanganyika, **361–373, 375–387.**
Anopheles gambiae, adult habits of, in East Africa, **199–242, 361–373, 375–387.**
Anopheles hispaniola, **445, 447–450, 452, 457, 458, 487.**
Anopheles hyrcanus, **446, 448, 449, 450, 453.**
Anopheles hyrcanus pseudopictus, **453.**
Anopheles implexus, **199, 225, 226.**
Anopheles labranchiae atroparvus, **438, 446, 448, 449, 450, 454.**
Anopheles labranchiae labranchiae, **444, 446, 448, 449, 450, 453–456, 458.**
Anopheles leesoni, **367, 368, 370.**
Anopheles machardyi, **363.**
Anopheles maculipennis, **438, 446, 448, 449, 450, 453–455.**
Anopheles marshalli, **367, 370.**
Anopheles marteri, **444, 446–451, 456, 457.**
Anopheles melanoon melanoon, **446, 448, 450, 453–456.**
Anopheles messeae, **438, 446, 448, 449, 450, 453–456.**
Anopheles nili, **367.**
Anopheles plumbeus, **444–451, 456, 457.**
Anopheles plumbeus corsicanus, **457.**
Anopheles rivulorum, **367, 368.**
Anopheles sacharovi, **444, 446, 448, 449, 450, 453, 454, 456.**
Anopheles seydeli, **370.**
Anopheles squamosus, **377.**
Anopheles sundaicus, **290.**
Anopheles superpictus, **446–450, 452, 457, 458, 487.**
Anoplocnemis curvipes, **107.**
Anoplolepis longipes, **105, 106, 107.**
Anthrenus fuscus, distribution and habits of, in Britain, **575–583.**
Anthrenus museorum, **575–577, 580.**
Anthrenus verbasci, distribution and habits of, in Britain, **575–583.**
Aphanogmus compressus, **246.**
Aphanostigma piri, bionomics of, in Israel, **631–634, 635.**
Aphidecta obliterata, **244, 245, 246, 255.**
Aphidoletes thompsoni, **245, 246, 257, 261.**
Aphis craccivora, **634, 777.**
Aphis fabae, method for estimating populations of, **751–756**; action of Systox on, **683–692, 701.**
Aphis farinosa, **771.**
Aphis gossypii, **634, 777–780.**
Aphis leguminosae (see *A. craccivora*).
Aphis pomi, **634.**
Aphis punicae, **634, 635, 636.**
Aphis ruborum, **635.**
Aphis saliceti (see *A. farinosa*).
apicalis, Culex.
apicoargenteus, Aëdes (*Stegomyia*).
Apis mellifera, **107.**
Aplastomorpha calandrae (see *Anisopteromalus*).
Apomecyna, systematic position of, **553.**
Apomecyna binubila, bionomics of, in Sudan, **553–561.**
Apomecyna cavifrons, **556.**
Apomecyna klugi, **556.**
Apomecyna latefasciata, **556.**
Apomecyna parumpunctata (*longipennis*), **556.**
Apomecyna scalaris, **556.**
Apomecyna senegalensis (see *A. binubila*).
Apple, Aphids on, **634, 635.**
Apricot, Aphids on, **623, 634.**
arcuatus, Syrphus.
arator, Hemiteles.
Areca catechu, Melittomma insulare on, **28.**

arenicola, Caenocrepis.
arguta, Alluaudinella.
Argyroploce leucotreta, **662, 673.**
Arthrocnodax, **772.**
artifrons, Orthellia (see *O. gemma*).
Arundo donax, Hyalopterus pruni on, **623.**
asiaticus, Aëdes pulchritarsis.
Aspidiotus destructor, **125.**
Aspongopus viduatus, **557.**
Atherigona aberrans, **792.**
Atherigona bedfordi, **792.**
Atherigona budongoana, **792.**
Atherigona excisa, **792.**
Atherigona ferruginea, **792.**
Atherigona griseiventris, **792.**
Atherigona haplopyga, **792.**
Atherigona nudiseta, **792.**
Atherigona steeleae, **792.**
Atherigona trapezia, **792.**
Atmospheric Pressure, effect of, on flight of *Aëdes aegypti*, **507–526.**
atomus, Paromicrus.
Atopogyne africana (see *Crematogaster*).
Atractocerus brevicornis, **2.**
atroparvus, Anopheles labranchiae.
Auchmeromyia, **785.**
aurantii, Toxoptera.
aureopyga, Orthellia.
auriculariae, Camptodiplosis.
aurites, Mansonia (*Taeniorhynchus, Coquillettidia*).
aurora, Ischnura.
Australia, *Carpophilus davidsoni* in, **389.**
autumnalis, Dixa; Musca.
Avocado, *Xyleborus morstatti* on, **707–710.**

B.

Baccha, **780.**
Balsam Woolly Aphid (see *Adelges piceae*).
balteata, Epistrophe.
Banana, *Pentalonia nigronervosa* on, **777.**
bancrofti, Wuchereria.
Barley, *Eurygaster integriceps* on, **497, 498.**
basicinctus, Culex.
Bauhinia tomentosa, Xyleborus morstatti on, **708.**
Bean Aphid, Black (see *Aphis fabae*).
Beans, Broad (see Broad Beans).
bedfordi, Atherigona.
Belep Islands, mosquitos in, **285–293.**
Bentonite, **297, 299, 300.**
Benzene Hexachloride (see BHC).
bergrothi, Helopeltis.
berlandi, Aëdes.
berolinensis, Phalacrotophora.
BHC, **47, 49–53, 55, 114, 137–139, 295–311, 419, 549, 606, 607, 639–646.**
bicruciatus, Coccus.
bimaculata, Cardiocondyla wroughtoni.
binubila, Apomecyna.
bipunctata, Diplacodes.
bipustulatus, Chilocorus.
Birds, insects and mites in nests of, **135–136, 576–579, 581.**
Bis(dimethylamino)fluorophosphine Oxide (see Dimefox).
bisetosa, Limnophora.
1:1-Bis(p-fluorophenyl)-2:2:2-trichloroethane (DFDT), **137–139.**
bisoctonotata, Thea.
bispinosa, Morellia.
bisselliella, Tineola.
bitaeniorhynchus, Culex.
bivittata, Lispe.
Box Shelters, for Anophelines, **363–365.**
Brachycaudus amygdalinus, bionomics of, in Israel, **628–631, 635, 636.**
Bracon deesae (see *Stenobracon*).
braminus, Typhlops.
brasiliense, Melittomma (*Hylecoetus*).
brassicae, Brevicoryne; Pieris.
brevicornis, Atractocerus.
Brevicoryne brassicae, action of Systox on, **684, 689–692.**
brevipalpis, Glossina.
Bridelia micrantha, relation of *Oecophylla longinoda* to other insects on, **97, 98, 104, 109, 114.**
Britain, household and stored products pests in, **351, 358, 389–402, 575–583;** insects and mites in birds' nests in, **135–136, 575–579, 581;** Cecidomyid parasites of Aphids and Psyllids in, **769, 770, 771.**
Broad Beans, estimating populations of Aphids on, **751–756;** used in experiments with systemic insecticide, **683–692.**
brumpti, Culex.
brunnipes, Stomoxys.
budongoana, Atherigona.
Bulrush (see *Arundo donax*).
buxtoni, Culex hilli; Mansonia (*Taeniorhynchus*).
Byomyia (see *Musca*).

C.

Cabbage, used in experiments with systemic insecticide, **683–692, 693–702.**
Cacao (*Theobroma cacao*), Aphids on, **98, 104, 777, 780;** Mirids on, **723–744;** Coreid known as *Theraptus* on, **431, 432;** *Xyleborus morstatti* on, **708;** relation of *Oecophylla longinoda* to other insects on, **98, 99, 104, 106, 109.**

Caenocrepis, Xenocrepis distinct from, **265.**
Caenocrepis arenicola, **265.**
caesar, Zenillia.
Calandra granaria, **640, 644.**
Calandra oryzae, control of, in stored maize, **295–311.**
calandrae, Anisopteromalus (*Aplastomorpha*).
calcitrans, Stomoxys.
caledonica, Tripteroides (*Mimeteomyia*).
Callirrhipis filiberti, **44.**
Camponotus, **739, 740.**
Camponotus grandidieri, **45.**
Camponotus maculatus, **45.**
Camptodiplosis auriculariae, **772.**
Canada, *Aëdes* spp. in, **67**; predators of *Adelges piceae* introduced into, **244, 272–275.**
canicularis, Fannia.
cantans, Aëdes.
Canthium zanzibaricum, *Oecophylla longinoda* and Coccids on, **98, 104, 109.**
capensis, Ophyra.
Carbon Dioxide, sensitivity of a strain of *Drosophila melanogaster* to, **315, 316, 323.**
Carcelia illota, **666.**
Cardiocondyla wroughtoni bimaculata, **107.**
Carpet Beetle, Varied (see *Anthrenus verbasci*).
Carpophilus, **305**; species of, associated with stored products in Britain, **389–402.**
Carpophilus davidsoni, **389, 392, 393, 394.**
Carpophilus dimidiatus, **389, 391–395, 400, 401.**
Carpophilus flavipes, **389, 390, 391, 393, 394.**
Carpophilus fumatus, **389, 392, 393, 395, 398, 399.**
Carpophilus hemipterus, **389, 391, 392, 394, 399, 400.**
Carpophilus humeralis, **389, 390, 391, 394, 399.**
Carpophilus immaculatus, **389.**
Carpophilus ligneus, **389, 391, 392, 394, 395, 402.**
Carpophilus maculatus, **389, 392, 393, 394, 399.**
Carpophilus marginellus, **389, 390, 391, 394, 401.**
Carpophilus mutilatus, **389, 391, 392, 393, 395, 397–399.**
Carpophilus niger, **389, 392, 393, 395.**
Carpophilus nitidus, **389, 390, 395, 396, 399.**
Carpophilus obsoletus, **389–395, 401, 402.**
Carpophilus pallipennis, **389, 392, 393, 395.**
Carpophilus sexpustulatus, **389, 390, 391, 394.**
Carpophilus succisus, **389, 390, 394, 396, 397, 399.**
Carulaspis visci, **247.**
Cashew (*Anacardium occidentale*), *Oecophylla longinoda* and Coccids on, **96, 98, 109**; new species of *Helopeltis* on, **703.**
caspius, Aëdes.
castanea, Crematogaster; Diparopsis.
castaneum, Melittomma (see *M. africanum*); *Tribolium.*
catori, Saissetia.
Cattle, *Glossina* and trypanosomiasis of, **415, 600**; relation of other flies to trypanosomiasis of, **784, 785**; use of DDT-treated, for control of *Glossina*, **411–421.**
caudatus, Ephialtes.
cavifrons, Apomecyna.
Cecidomyella, **772.**
Cecidomyids, as endoparasites, **769.**
Centistes fuscipes, **267.**
Centistes lucidator, **267.**
Centistes scymni, sp.n., **246, 256, 267–270, 272, 273.**
centurionis, Chrysops (*Kleineana*).
cephalonica, Corcyra.
Cerataphis lataniae, **98, 104, 106.**
Ceratocystis, **14.**
cerealella, Sitotroga.
Cereals, Stored, pests of, and their control, **295–311, 341–350, 351, 399, 400, 401, 639–646.**
ceriferus, Ceroplastes.
Ceroplastes ceriferus, **105.**
Ceroplastes rubens, **105.**
Certhia familiaris, **272.**
Chaitophorus salicti, **771.**
Chaoborus, **438, 439.**
Chaoborus astictopus, **441.**
Chaoborus crystallinus, **441, 442, 443.**
Chaoborus flavicans, **441, 442, 443.**
Chaoborus pallidus, **441, 442, 443.**
Chilo zonellus, **647–651, 653–657.**
Chilocorus bipustulatus, **635.**
Chilocorus wahlbergi, **126.**
Chromaphis juglandicola, **635.**
Chrysodiplosis, **772.**
chrysogaster, Eretmapodites.
Chrysomphalus dictyospermi, **105.**
Chrysopa ventralis, **245, 246, 257, 261, 271.**
Chrysops centurionis, **200, 229, 233.**
Cinacium iaksuiense, **631, 637.**
Cinchona, new species of *Eucerocoris* on, **705.**
cinereus, Aëdes.

Cinnamon, Coreid known as *Theraptus* on, **431**.
citri, Planococcus.
citriculus, Pseudococcus.
Citrus, Aphids on, **98**, **104**, **634**, **635**, **777**; Coccids on, **98**, **104**; *Oecophylla longinoda* on, **98**, **100**, **104**, **109**.
Cladosporium cladosporiodes, **708**.
claviger, Anopheles.
Clerodendron, Xyleborus morstatti on, **708**.
Clove (*Jambosa caryophyllus*), *Oecophylla longinoda* and Coccids on, **97–101**, **104**, **105**, **107**, **108**, **109**, **113–127**.
Cnemodon latitarsis, **245**, **246**, **257**, **271**.
Cnidocampa flavescens (see *Monema*).
Coca (see *Erythroxylon coca*).
Coccinella conglobata, **635**.
Coccinella septempunctata, **246**, **635**.
coccinellae, Tetrastichus.
Coccophagus, **123**, **124**, **125**, **130**.
Coccophagus nigritus, **123**, **126**.
Coccus acuminatus, **105**.
Coccus africanus, **105**.
Coccus bicruciatus, **105**.
Coccus elongatus, **97**.
Coccus hesperidum, **96**, **97**, **98**, **104**, **105**.
Coccus viridis, **96**, **97**, **98**, **104**, **105**.
cochleariae, Phaedon.
Coconut (*Cocos nucifera*), *Melittomma insulare* on, **1–66**; Coreid known as *Theraptus* on, **108**, **109**, **429–432**, **433–435**; relation of *Oecophylla longinoda* to other insects on, **98–101**, **104**, **107–110**, **125**, **126**.
coffeae, Saissetia.
Coffee (*Coffea* spp.), *Oecophylla longinoda* and Coccids on, **98**, **109**; *Xyleborus morstatti* on, **708**.
Cold-hardiness, factors influencing, in caterpillars, **329–339**; of *Laemophloeus minutus*, **351–359**.
collinus, Diplazon prope.
Colocynthis citrullus (see Watermelon).
Coloured Cloths, responses of *Aëdes* spp. to, **67–78**.
communis, Aëdes.
compressus, Aphanogmus.
conducens, Musca (*Byomyia*).
confusum, Tribolium.
confusus, Xyleborus.
conglobata, Coccinella.
Congo, Belgian, *Glossina brevipalpis* in, **501–505**.
congolense, Trypanosoma.
conspersus, Diaecoderus.
Cook Islands, mosquitos in, **423–427**.
Coquillettidia (see *Mansonia*).
Corcyra cephalonica, **647**, **648**, **653–657**.
cornutus, Gnathocerus.
Corsica, mosquitos of, **437–494**.
corsicanus, Anopheles plumbeus.
costimacula, Eublemma.
Cotton (*Gossypium*), *Diparopsis* spp. on, **661–681**.
coustani, Anopheles.
craccivora, Aphis.
crassipes, Mansonia (*Coquillettidia*).
crassirostris, Musca (*Philaematomyia*).
Crematogaster africana, **740**.
Crematogaster castanea, **115**.
Crematogaster striatula, **740**.
Cremifania nigrocellulata, **244**, **245**, **246**, **255**, **257**.
cremifaniae, Pachyneuron.
Crotalaria, Xyleborus morstatti on, **708**.
Cryptus sexannulatus, **531**.
crystallinus, Chaoborus.
Ctenarytaina, **106**.
Culex, **438**, **445**.
Culex annulirostris, **280**, **286**, **287**, **288**, **290**, **291**, **424**, **425**, **426**.
Culex apicalis, **485**.
Culex basicinctus, **286**, **287**.
Culex bitaeniorhynchus, **286–290**.
Culex brumpti, **481**, **483**.
Culex fatigans (see *C. pipiens fatigans*).
Culex fraudatrix, **289**, **291**.
Culex hilli buxtoni, **291**.
Culex hortensis, **482–487**.
Culex impudicus, **443**, **482–486**.
Culex laticinctus, **482**, **483**, **486**.
Culex mimeticus, **458**, **482**, **483**, **486**.
Culex modestus, **482**, **483**, **486**, **487**.
Culex pacificus, **291**, **292**.
Culex pipiens, **482**, **483**, **486**, **488**.
Culex pipiens fatigans, **286**, **287**, **291**, **292**, **293**, **377**, **424**, **425**, **426**; ryanodine against, **403–410**.
Culex prosecutor, **444**, **487**.
Culex pseudomelanoconia, **286–289**.
Culex pseudomimeticus (see *C. prosecutor*).
Culex quinquefasciatus, auct. (see *C. pipiens fatigans*).
Culex sinaiticus, **485**.
Culex sitiens, **286**, **287**, **290**.
Culex theileri, **482**, **483**, **486**, **488**.
Culex univittatus, **483**.
Cucumis melo (see Melon).
Cucurbita pepo (see Vegetable Marrow).
Culiseta, **438**, **445**.
Culiseta annulata, **459**, **460**, **461**, **464**, **465**.
Culiseta fumipennis, **444**, **459–463**.
Culiseta litorea, **460**, **462**, **463**.
Culiseta longiareolata, **459**, **460**, **461**, **463**, **464**.
Culiseta morsitans, **460–464**.
Culiseta subochrea, **438**, **459**, **460**, **461**, **464**.

curvipes, Anoplocnemis.
cuthbertsoni, Musca.
Cydia pomonella, **531.**
cyptopus, Hodgesia.

D.

Dactylosternum abdominale, **44.**
davidsoni, Carpophilus.
DDT, **83, 85, 86–88, 90, 297, 299, 301, 302, 323–328, 413, 415, 419, 591, 592, 594, 597, 601, 615, 639–646, 745.**
Deckenia nobilis, Melittomma insulare on, **28.**
deesae, Stenobracon (*Bracon*).
demeilloni, Anopheles.
Dendrobium veratrifolium, Xyleborus morstatti on, **708.**
dendrophilus, Aëdes (*Stegomyia*).
destructor, Aspidiotus.
detorquens, Technomyrmex.
detritus, Aëdes.
DFDT, **137–139.**
Diaecoderus conspersus, **107.**
Diatomite, **297–300, 302–308.**
Dichaetomyia albivitta, **791.**
Dichaetomyia fumaria, **791.**
Dichaetomyia liberia, **791.**
Dichaetomyia pallidula, **791.**
Dichaetomyia quadrata nubiana, **791.**
Dichaetomyia serena, **791.**
p-Dichlorobenzene, **47–53, 55.**
dictyospermi, Chrysomphalus.
Dieldrex, **49–53, 55, 57, 58.**
Dieldrin, **49–53, 55, 57, 58, 419.**
Diethyl Ethylmercaptoethyl Thiophosphate, **59**; mixtures of isomers of, in Systox (*q.v.*), **683, 693.**
Diethyl p-Nitrophenyl Phosphate (see Paraoxon).
Dimefox (Bis(dimethylamino)fluorophosphine Oxide), **59, 686.**
Dimethyl Phthalate, **286.**
dimidiatus, Carpophilus.
Dimorphia tristis, **791.**
Dinitro-o-cresol (see DNC).
Diocalandra frumenti, **43.**
Diparopsis castanea, **661, 665, 669, 670, 679.**
Diparopsis watersi (*perditor*), bionomics of, in northern Nigeria, **661–681.**
Diplacodes bipunctata, **424.**
Diplazon annulatus, **246.**
Diplazon fissorius, **246.**
Diplazon ornatus, **246.**
Diplazon prope collinus, **246.**
Diplazon tarsatorius, **246.**
Distantiella theobroma, bionomics of, in Gold Coast, **723–744.**
distincta, Pyrellina.
Dixa, **437, 438.**
Dixa amphibia, **440.**
Dixa autumnalis, **440.**
Dixa laeta, **440.**
Dixa nebulosa, **440.**
Dixa puberula, **440.**
Dixa serrifera, **440.**
Dixa submaculata, **440.**
DNC, **177–197.**
domestica, Musca.
dominica, Rhizopertha.
Dorylus nigricans, **107.**
Drepanosiphum platanoides, **769.**
Dreyfusia, **244** (note).
Drosophila, as host for *Spalangia drosophilae*, **527–533, 535.**
Drosophila melanogaster, rearing and use of, for insecticide tests, **313–316, 317–321, 323–328.**
drosophilae, Spalangia.
Duranta plumieri, Aphis punicae on, **634, 635.**
Dusts, Inert, against pests of stored maize, **295–311.**
Dysdercus superstitiosus, **662.**

E.

E1059, active ingredient of Systox (*q.v.*), **683.**
Earias, **662, 673.**
echinus, Aëdes.
Echthrolaricobius paradoxus, **246.**
Egg-plant, *Aphis gossypii* on, **777.**
Elachista, **267.**
Elaeis, Xyleborus morstatti on, **708.**
elongatus, Coccus.
Endaphis perfidus, **769, 772, 774.**
endogena, Endopsylla.
Endopsylla, **772.**
Endopsylla agilis, **770, 771, 774.**
Endopsylla endogena, **770, 771.**
Ephestia kuehniella, **531.**
Ephialtes caudatus, **531.**
Epistrophe balteata, **246.**
eremophila, Anaclysta.
Eretmapodites, **239.**
Eretmapodites chrysogaster, **200, 201, 213, 214, 215, 238.**
erichsonii, Laricobius.
Erythrina, Xyleborus morstatti on, **708.**
Erythroxylon coca, Xyleborus morstatti on, **708.**
Eublemma costimacula, **126.**
Eublemma pyrochroa, **126.**
Eublemma scitula, **126.**
Euborellia plebeja, **44.**
Eucalymnatus tessellatus, **97, 105.**
Eucerocoris festivus, sp.n., **705.**
Eucerocoris horvathi, **705.**
Eulecanium, **97, 105, 124** (note).

Eumusca (see *Musca*).
Euphorus sahlbergellae, **738.**
Euponera sennaarensis, **787.**
Eurygaster integriceps, control of, in Syria, **495–500.**
excisa, *Atherigona* (*Acritochaeta*).
exigua, *Lyperosia*.
Exochomus, **126.**
Exochomus flavipes, **635.**
Exochomus quadripustulatus, **244, 246, 635.**

F.

fabae, *Aphis*.
falciparum, *Plasmodium*.
Fannia canicularis, **792.**
Fannia suturalis, **792.**
farauti, *Anopheles*.
farinosa, *Aphis*.
fasciata, *Musca* (*Byomyia*).
fatigans, *Culex pipiens*.
ferrièrei, *Pachyneuron*.
ferruginea, *Atherigona*.
ferrugineus, *Laemophloeus*.
festivus, *Eucerocoris*.
Figulus striatus, **44.**
Fiji, *Xyleborus morstatti* in, **708.**
filiberti, *Callirrhipis*.
Finlaya (see *Aëdes*).
fissorius, *Diplazon*.
fitchi, *Aëdes*.
flavescens, *Gymnodia; Monema* (*Cnidocampa*); *Pantala*.
flavicans, *Chaoborus*.
flaviceps, *Alluaudinella*.
flavipes, *Carpophilus; Exochomus; Helorus*.
Flour, used in rearing insects, **137, 341–350**; fumigation of, **639–646.**
foersteri, *Psylla*.
formosum, *Pachyneuron*.
foveicollis, *Rhaphidopalpa*.
France, Cecidomyid parasite of *Drepanosiphum platanoides* in, **769**; *Pullus impexus* and *Adelges piceae* in, **244, 251, 252.**
fraudatrix, *Culex* (*Lophoceratomyia*).
frit, *Oscinella*.
frumenti, *Diocalandra*.
fumaria, *Dichaetomyia*.
fumatus, *Carpophilus*.
Fumigation, responses of pests to, **47–53, 137–139, 639–646.**
fumipennis, *Culiseta*.
fumosa, *Xylena*.
funestus, *Anopheles*.
fur, *Ptinus*.
fuscipes, *Centistes; Glossina palpalis*.
fuscopennata, *Mansonia* (*Taeniorhynchus*, *Coquillettidia*).
fuscus, *Anthrenus*.

G.

gambiae, *Anopheles* (*Myzomyia*).
Gambusia, **424, 425.**
Gammalin, **50–53, 55.**
gemma, *Orthellia*.
geniculata, *Mydaea*.
geniculatus, *Aëdes; Glycyphagus*.
Germany, *Pullus impexus* and *Adelges piceae* in, **243–278**; Cecidomyid parasites of Aphids and Psyllids in, **770, 771.**
Gerris, **424.**
Gliricidia sepium, *Aphis craccivora* on, **777.**
Glossina brevipalpis, **144, 163, 172, 173**; bionomics of, in Belgian Congo, **501–505.**
Glossina longipennis, **144, 172.**
Glossina morsitans, **501, 502, 504, 568, 569, 615, 619, 783**; measures against, **411–421, 585–603, 605–612, 617, 620.**
Glossina pallidipes, **411, 413, 415**; ecology of, in Kenya, **141–161, 163–174**; measures against, **585–603.**
Glossina palpalis, **504**; incidence of trypanosomes in, in Sierra Leone, **797–801**; anatomy of tarsi of, **719.**
Glossina palpalis fuscipes, **790**; measures against, **413, 563–574.**
Glossina swynnertoni, **568, 569**; measures against, **411–421, 585–603, 605–612, 613–622.**
Glossina tachinoides, **783.**
Glossinella minuta (see *Lyperosia*).
Glycyphagus geniculatus, **135, 136.**
Gnathocerus cornutus, **305, 307.**
Gold Coast, Mirids on cacao in, **723–744.**
gossypiella, *Platyedra*.
gossypii, *Aphis*.
Gossypium (see Cotton).
granaria, *Calandra*.
grandidieri, *Camponotus*.
grandis, *Mythimna*.
gregaria, *Schistocerca*.
griseiventris, *Atherigona*.
griseola, *Leucopis*.
Groundnuts, Stored, fumigation of, **639–646**; *Carpophilus* spp. in, **400, 402.**
Guava, insects on, **431, 432, 634.**
Guiana, British, *Culex pipiens fatigans* in, **403–410.**
Gymnodia, **785.**
Gymnodia flavescens, **791.**
Gymnodia mervinia, **791.**

H.

haematoda, *Odontomachus*.
haplopyga, *Atherigona*.

Helopeltis anacardii, sp.n., **703.**
Helopeltis bergrothi, **107.**
Helopeltis schoutedeni, **705.**
Helorus flavipes, **246.**
Hemerobius nitidulus, **244.**
Hemerobius stigma, **244.**
Hemiberlesia lataniae, **125.**
Hemiberlesia palmae, **105.**
hemipterus, Carpophilus.
Hemiteles areator, **246.**
hesperidum, Coccus.
heterochaeta, Passeromyia.
1:2:3:4:11:11-Hexachloro-1:4:5:8:9:10-hexahydro-1: 4: 5: 8-endo-exo-dimethylene-naphthalene (see Aldrin).
Hexacola, **531.**
Hexamermis, **246, 271.**
hilli, Culex.
hirtellus, Ptinus.
hispaniola, Anopheles.
Histiostoma, **43.**
Hodgesia cyptopus, **199, 219–222.**
Holland, Cecidomyid parasites of Aphids in, **771.**
Honey Bee (see *Apis mellifera*).
Horsetail Knotweed (see *Polygonum equisetiforme*).
hortensis, Culex.
horvathi, Eucerocoris.
House-fly (see *Musca domestica*).
Houses, habits of Anophelines in relation to, in Tanganyika, **361–373, 375–387.**
humeralis, Carpophilus.
humilis, Musca.
Hyalopterus pruni, bionomics of, **623–628, 635, 636.**
Hydrotaea polita, **791.**
hygrophanus, Pleurotus.
Hylecoetus (see *Melittomma*).
Hyperaspis senegalensis, **265.**
hyrcanus, Anopheles.

I.

iaksuiense, Cinacium.
Icerya seychellarum, **98, 104, 105, 708.**
iceryoides, Phenacoccus.
illota, Carcelia.
immaculatus, Carpophilus.
impexus, Pullus.
implexus, Anopheles.
impudicus, Culex.
inday, Phenacaspis.
India, *Stenobracon deesae* parasitising Lepidoptera in, **647–659**; *Xyleborus morstatti* in, **708.**
Indo-China, *Xyleborus morstatti* in, **708.**
Indonesia, mosquitos in, **290**; *Xyleborus morstatti* in, **708.**
ingrami, Aëdes (*Finlaya*).
Insecticides, aircraft application of, **79–92, 177, 585–603, 605–612, 613–622, 745–749**; temperature and effectiveness of, **137–139**; apparatus for applying small measured doses of, **317–321**; studies concerning uptake of contact, **711–722.**
insulare, Melittomma.
integriceps, Eurygaster.
inventrix, Pyrellina.
Iphiaulax, **560.**
irritans, Aëdes (*Aëdimorphus*).
Ischnura aurora, **424.**
Israel, fruit-tree Aphids in, **623–638.**
Isthmia, **96, 105.**
Italy, *Pullus impexus* in, **251, 252.**
Iulomorpha, **44.**

J.

jaceae, Macrosiphum.
Jambosa caryophyllus (see Clove).
Japan, *Monema flavescens* in, **329.**
Java (see Indonesia).
juglandicola, Chromaphis.

K.

Kenya Colony, *Glossina* spp. in, **141–161, 163–174, 563–574**; mosquitos in, **200, 201, 207, 225, 227**; control of *Onchocerca* by eradication of *Simulium neavei* in, **175–176**; *Oecophylla longinoda* in, **94, 98**; parasite of *Hyperaspis senegalensis* in, **265**; pests of stored maize in, **295–311.**
kermorganti, Aëdes (*Mucidus*).
Kleineana centurionis (see *Chrysops*).
klugi, Apomecyna.
kuehniella, Ephestia.

L.

laboriosa, Polyrachis (*Myrma*).
labranchiae, Anopheles.
Laemophloeus, **305.**
Laemophloeus ferrugineus, **341, 344, 345, 346, 348.**
Laemophloeus minutus, effects of diet on life-history of, **341–350**; effects of low temperature on, **351–359.**
Laemophloeus pusilloides, **341, 345.**
Laemophloeus turcicus, **341.**
laeta, Dixa.
Laricobius erichsonii, **244, 245, 246, 255, 261.**
Lasiopticus seleniticus, **636.**
lataniae, Cerataphis; Hemiberlesia.
latefasciata, Apomecyna.

laticinctus, Culex.
laticollis, Neotermes.
latitarsis, Cnemodon.
latro, Ptinus.
laxifrons, Orthellia.
leesoni, Anopheles.
leguminosae, Aphis (see *A. craccivora*).
Leiophron, **267.**
Lephthyphantes obscurus, **246.**
lepidonotus, Aëdes.
Lepidopterous Larvae, freezing process in frost-hardy, **329–339.**
Leucophaea surinamensis, **44.**
Leucopis griseola, **245, 246.**
Leucopis (*Leucopomyia*) *obscura*, **244, 245, 246, 255, 257, 261.**
Leucopis puncticornis, **636.**
Leucopomyia obscura (see *Leucopis*).
leucospila, Lispe.
leucotreta, Argyroploce.
liberia, Dichaetomyia.
ligneus, Carpophilus.
Limax maximus, **246.**
Limax tenellus, **246.**
Limnogonus, **424.**
Limnophora bisetosa, **791.**
Limnophora notabilis, **791.**
Limnophora obsignata, **791.**
Limnophora rufimana, **791.**
Limnophora translucida, **791.**
lineata, Mydaea.
Lispe bivittata, **792.**
Lispe leucospila, **792.**
Lispe modesta, **792.**
Lispe nivalis, **792.**
Lispe nuba, **792.**
Lispe pygmaea, **792.**
litorea, Culiseta.
Locust, Desert (see *Schistocerca gregaria*).
longiareolata, Culiseta.
longinoda, Oecophylla.
longipalpis, Aëdes (*Finlaya*).
longipennis, Apomecyna (see *A. parumpunctata*)*; Glossina.*
longipes, Anoplolepis.
longitubus, Aëdes.
Lophoceratomyia (see *Culex*).
Loxostege sticticalis, **531.**
Loxotropa, **531.**
lucidator, Centistes.
lucidula, Musca (*Byomyia*).
Lucilia, **786.**
lusoria, Musca (*Eumusca*).
Lygocerus piceae, **246.**
Lyperosia exigua, **790.**
Lyperosia minuta, **790.**
Lyperosia potans (see *L. thirouxi*).
Lyperosia spinigera, **783, 790.**
Lyperosia thirouxi, **790.**

M.

machardyi, Anopheles.
Macromischoides aculeatus, **739, 740, 741.**
Macrosiphum jaceae, **770.**
maculans, Pseudendaphis.
maculatus, Camponotus; Carpophilus.
maculinervis, Mydaea (*Myiospila*).
maculipennis, Anopheles.
maculisquama, Orthellia.
Madagascar, *Melittomma insulare* in, **2, 8, 10, 18, 24, 28–32, 35, 36, 37, 45, 61**; *Xyleborus morstatti* in, **708.**
mahéensis, Nasutitermes.
mahenus, Alaus.
Mahogany, *Xyleborus morstatti* on, **708.**
Maize, Stored, treatments against insects in, in Kenya, **295–311**; used for rearing *Laemophloeus minutus*, **341–350**; *Carpophilus* spp. in, **399.**
Malaria, and *Anopheles* in New Hebrides, **279–283, 290.**
malariae, Plasmodium.
mali, Psylla.
Mango, insects on, **431, 432, 708.**
Mangrove, *Oecophylla longinoda* associated with, **127.**
Mansonia (*Taeniorhynchus*), **207, 239, 444, 445.**
Mansonia (*Taeniorhynchus*) *africana*, **199, 215–218, 229, 239, 377.**
Mansonia (*Taeniorhynchus*) *aurites*, **199, 230.**
Mansonia (*Taeniorhynchus*) *buxtoni*, **466, 467.**
Mansonia crassipes, **286.**
Mansonia (*Taeniorhynchus*) *fuscopennata*, **199, 230.**
Mansonia (*Taeniorhynchus*) *pseudoconopas*, **199, 224, 230.**
Mansonia (*Taeniorhynchus*) *richiardii*, **438, 466, 467.**
Mansonia (*Taeniorhynchus*) *uniformis*, **377.**
Mansonioides (see *Mansonia*).
marginellus, Carpophilus.
marginipennis, Orthellia.
mariae, Aëdes.
marshalli, Anopheles.
marteri, Anopheles.
mauritanicus, Tenebroides.
Mauritius, *Xyleborus morstatti* in, **708.**
Mecynapus (see *Apomecyna*).
megacephala, Pheidole.
melancephalum, Tapinoma.
melanogaster, Drosophila.
melanoneura, Psylla.
melanoon, Anopheles.
Melia azedarach, *Xyleborus morstatti* on, **708.**

Meliola, **119.**
Melittomma (*Hylecoetus*) *africanum*, **1.**
Melittomma albitarsis, **4.**
Melittomma (*Hylecoetus*) *brasiliense*, **1, 4.**
Melittomma castaneum (see *M. africanum*).
Melittomma insulare, biology and control of, in Seychelles, **1–66.**
Melittomma sericeum, **4, 5.**
mellifera, Apis.
Melon, Coleoptera on, **553, 557, 558, 560.**
Mermis, **271.**
mervinia, Gymnodia.
mesnili, Scymnophagus.
mespiliella, Ovatus.
messeae, Anopheles.
Methyl Bromide, **303, 305.**
mexicana, Xenocrepis.
Microcerotermes subtilis, **44.**
Microvelia oceanica, **424.**
Mimeteomyia caledonica (see *Tripteroides*).
mimeticus, Culex.
minuta, Lyperosia (*Glossinella*).
minutus, Laemophloeus.
Mochlonyx, **441.**
modesta, Lispe.
modestus, Culex.
Monema (*Cnidocampa*) *flavescens*, studies on cold-hardiness in larvae of, **329–339.**
monoceros, Oryctes.
Morellia abyssinica (see *M. prolectata*).
Morellia bispinosa, **785.**
Morellia paradoxa, **785.**
Morellia prolectata, **785.**
Morellia smaragdina, **785.**
morsitans, Culiseta; Glossina.
morstatti, Xyleborus.
Mosquitos, studies on adult habits of African, **199–242, 361–373, 375–387**; in Pacific Islands, **279–283, 285–293, 423–427**; of Sardinia and Corsica, **437–494**; ryania against larvae of, **403–410** (see also under *Aëdes*).
Mucidus (see *Aëdes*).
Musca, **530, 785, 786, 792.**
Musca albina albina, **788.**
Musca alpesa (see *M. lusoria*).
Musca autumnalis, **787, 789.**
Musca conducens, **787, 788.**
Musca crassirostris, **787, 788.**
Musca cuthbertsoni, **787.**
Musca domestica, **531, 787, 788**; anatomy of tarsi of, **718–719.**
Musca domestica vicina, **783, 787, 788, 789.**
Musca fasciata, **787, 788.**
Musca humilis, **788.**
Musca lucidula, **787, 788.**
Musca lusoria, **789.**
Musca nebulo, **787.**
Musca sorbens (*primitiva*), **788.**
Musca sorbens alba, **788.**
Musca tempestatum, **787, 788.**
Musca tempestiva, **787, 788.**
Musca vitripennis, **787.**
Musca xanthomelas, **787, 789.**
museorum, Anthrenus.
mutilatus, Carpophilus.
Mydaea geniculata, **791.**
Mydaea lineata, **791.**
Mydaea maculinervis, **791.**
Myrma laboriosa (see *Polyrachis*).
Myrobalan, *Myzus persicae* on, **634.**
Mysore (see India).
Mythimna grandis, cold-hardiness of larvae of, **335.**
Mythimna turca, **335.**
Myzomyia (see *Anopheles*).
Myzus persicae, action of Systox on, **684, 689–692**; food-plants of, **634.**

N.

Nasutitermes mahéensis, **44.**
neavei, Simulium.
nebulo, Musca.
nebulosa, Dixa.
Neoculex (see *Culex*).
Neomysia oblongoguttata, **246.**
Neotermes laticollis, **44.**
Nephrosperma vanhoutteana, *Melittomma insulare* on, **27.**
Netherlands (see Holland).
New Caledonia, mosquitos in, **285–293.**
New Guinea, new Mirid on *Cinchona* in, **705.**
New Hebrides, *Anopheles* and malaria in, **279–283, 290.**
niger, Carpophilus.
Nigeria, *Diparopsis* spp. in, **661–681.**
nigerrimus, Aëdes (*Mucidus*).
nigra, Saissetia; Stomoxys.
nigricans, Dorylus (*Anomma*).
nigritus, Coccophagus.
nigrocellulata, Cremifania.
nigrocincta, Orthellia (see *O. nudissima*).
nigronervosa, Pentalonia.
nili, Anopheles.
nitidulus, Hemerobius.
nitidus, Carpophilus.
nivalis, Lispe.
nordmannianae, Adelges.
notabilis, Limnophora.
notoscriptus, Aëdes (*Finlaya*).
nuba, Lispe.
nubiana, Dichaetomyia quadrata.
nubilalis, Pyrausta.

nudiseta, Atherigona.
nudissima, Orthellia.
nüsslini, Adelges (see *A. nordmannianae*).
Nyasaland, *Diparopsis castanea* in, **665, 666, 668, 670.**

O.

obliterata, Aphidecta.
oblongoguttata, Neomysia.
obscura, Leucopis (*Leucopomyia*).
obscurus, Lephthyphantes.
obsignata, Limnophora.
obsoletus, Carpophilus.
oceanica, Microvelia.
ocellata, Anatis.
Ochlerotatus (see *Aëdes*).
Ochromusca trifaria, **785.**
Octamethyl Pyrophosphoramide (see Schradan).
Odontomachus haematoda, **41, 42, 45.**
Oecophylla longinoda, bionomics and relations to other insects of, **93–112, 113–134, 431, 432, 739–742.**
Oecophylla longinoda textor, **94, 95.**
Oecophylla smaragdina, **94, 108.**
Oil Palm (see *Elaeis*).
oleae, Parlatoria; Saissetia.
Oligotoma scottiana, **44.**
Onchocerca volvulus, **175, 176.**
Ophyra capensis, **791.**
ornatus, Diplazon.
Orthellia albigena, **786.**
Orthellia artifrons (see *O. gemma*).
Orthellia aureopyga, **786.**
Orthellia gemma, **786.**
Orthellia laxifrons, **786.**
Orthellia maculisquama, **786.**
Orthellia marginipennis, **786.**
Orthellia nudissima (*nigrocincta*), **786.**
Orthellia racilia, **786.**
Orthellia splendida, **786.**
Orthopodomyia, **438.**
Orthopodomyia pulchripalpis, **444, 445, 465.**
Oryctes monoceros, **21, 25, 44.**
oryzae, Calandra.
Oryzaephilus surinamensis, **137–139, 305, 642.**
Oscinella frit, **531.**
Otacustes ruficollis, **246.**
Ovatus mespiliella, **634.**

P.

Pachyneuron cremifaniae, **246.**
Pachyneuron ferrièrei, **246.**
Pachyneuron formosum, **246.**
pacificus, Culex.
pallidipes, Glossina.
pallidula, Dichaetomyia.
pallidus, Chaoborus.
pallipennis, Carpophilus.
palmae, Hemiberlesia.
palpalis, Glossina.
Paltothyreus tarsatus, **107, 108.**
Pantala flavescens, **424.**
paradoxa, Morellia.
paradoxus, Echthrolaricobius.
paramaribensis, Acropyga.
Paraoxon, **686, 695–699, 701.**
Paraputo ritchiei, **105.**
Parathion, **59, 495–500.**
Parlatoria oleae, **633.**
Parlatoria proteus, **105.**
Paromicrus atomus, **44.**
parumpunctata, Apomecyna.
Passeromyia heterochaeta, **783, 786.**
Peach, *Hyalopterus pruni* on, **623.**
Pear, Aphids on, **631–635.**
Pemba, Coreid known as *Theraptus* in, **433–435.**
pembaensis, Aëdes (*Skusea*).
Penicillium pallidum, **708.**
Pentalonia nigronervosa, **777, 778, 780.**
perditor, Diparopsis (see *D. watersi*).
peregrina, Psylla mali.
perfidus, Endaphis.
perforans, Xyleborus.
Persea americana (see Avocado).
persicae, Myzus.
petragnani, Anopheles claviger.
Phaedon cochleariae, experiments with Systox against, **693–702.**
Phaenobremia, **635.**
Phalacrotophora berolinensis, **246.**
Phaonia abnormis, **791.**
Pheidole, **740.**
Pheidole megacephala, **431, 739.**
Pheidole punctulata, **105–108, 115.**
Phenacaspis inday, **125.**
Phenacoccus iceryoides, **96, 97, 106.**
Philaematomyia (see *Musca*).
Phormia terraenovae, anatomy of tarsi of, **711–718.**
Phragmites communis (Reed), *Hyalopterus pruni* on, **623–627, 635, 636.**
Phytodietus pulcherrimus, **531.**
piceae, Adelges; Lygocerus.
Pieris brassicae, experiments with Systox against, **693–702.**
Pineus, **244** (note).
pionips, Aëdes.
Piperonyl Butoxide, **305–308.**
pipiens, Culex.
piri, Aphanostigma; Stephanitis (see *S. pyri*).
Planococcus citri, **98.**
plantaginea, Sappaphis.
Plasmodium, **280, 292.**
Plasmodium falciparum, **281.**

Plasmodium malariae, **281, 282.**
Plasmodium vivax, **281.**
platanoides, Drepanosiphum.
Platyedra gossypiella, **662, 673.**
plebeja, Euborellia.
Pleurotus hygrophanus, **14.**
Plum, Japanese, Aphids on, **634.**
plumbeus, Anopheles.
polita, Hydrotaea.
Polygonum equisetiforme, *Brachycaudus amygdalinus* on, **628.**
polynesiensis, Aëdes (Stegomyia).
Polyrachis laboriosa, **740.**
Pomegranate (*Punica*), Aphids on, **634, 635.**
pomi, Aphis.
pomonella, Cydia.
Portugal, Cecidomyid parasite of *Stephanitis pyri* in, **770.**
potans, Lyperosia (see *L. thirouxi*).
praeteritus, Aëdes.
primitiva, Musca (see *M. sorbens*).
prolectata, Morellia.
prope, Diplazon.
Propylea quatuordecimpunctata, **246.**
prosecutor, Culex.
proteus, Parlatoria.
Protophormia terraenovae (see *Phormia*).
pruni, Hyalopterus.
Pseudendaphis maculans, gen. et sp.n., parasite of Aphids in Trinidad, **772–774, 777–781**; bionomics of, **777–781.**
Pseudococcus, **96, 97.**
Pseudococcus adonidum, **105.**
Pseudococcus citriculus, **98, 104.**
pseudoconopas, Mansonia (Taeniorhynchus, Coquillettidia).
pseudomelanoconia, Culex (Neoculex).
Pseudomicrella salicti (see *Chaitophorus*).
pseudomimeticus, Culex (see *C. prosecutor*).
pseudopictus, Anopheles hyrcanus.
pseudorusticus, Aëdes.
pseudoscutellaris, Aëdes (Stegomyia).
psidii, Pulvinaria.
Psylla foersteri, **770.**
Psylla mali, **770, 771.**
Psylla mali peregrina, **770.**
Psylla melanoneura, **770.**
Psylla pyricola, **770.**
Pullus impexus, bionomics and parasites of, **243–278.**
Pulvinaria psidii, **105.**
Punica (see Pomegranate).
Ptinus fur, **135.**
Ptinus hirtellus, **135.**
Ptinus latro, **135.**
Ptinus pusillus, **135.**
Ptinus sexpunctatus, **135.**
Ptinus subpilosus, **135.**
Ptinus tectus, **135.**
puberula, Dixa.
pulcherrimus, Phytodietus.
pulchripalpis, Orthopodomyia.
pulchritarsis, Aëdes.
puncticornis, Leucopis.
punctor, Aëdes.
punctulata, Pheidole.
punicae, Aphis.
pura, Xenocrepis.
pusilloides, Laemophloeus.
pusillus, Ptinus.
pygmaea, Lispe.
pyramidea, Amphipyra.
Pyrausta nubilalis, **531**; cold-hardiness of larvae of, **335.**
Pyrellia scintillans, **786.**
Pyrellia spinthera, **786.**
Pyrellina distincta, **792.**
Pyrellina inventrix, **792.**
Pyrellina ruficauda, **792.**
Pyrethrins (or Pyrethrum), **295–311, 378.**
pyri, Stephanitis.
pyricola, Psylla.
pyrochroa, Eublemma.
Pyrophorus, **44.**

Q.

quadrata, Dichaetomyia.
quadripustulatus, Exochomus.
quasirusticus, Aëdes.
quatuordecimpunctata, Propylea.
Quince, Aphids on, **634.**
quinquefasciatus, auct., *Culex* (see *C. pipiens fatigans*).

R.

racilia, Orthellia.
Raphidia, **246.**
refiki, Aëdes.
regularis, Scydmaenus.
Retithrips syriacus, **635.**
Rhaphidopalpa foveicollis, **557, 560.**
Rhizopertha dominica, **305.**
richiardii, Mansonia (Taeniorhynchus).
ritchiei, Paraputo.
rivulorum, Anopheles.
Roscheria melanochetes, *Melittomma insulare* on, **28.**
Ruanda-Urundi (see Congo, Belgian).
rubens, Ceroplastes.
ruborum, Aphis.
Rubus ulmifolius, *Aphis ruborum* on, **635.**
Rucide, **413.**
ruficauda, Pyrellina.
ruficollis, Otacustes.

rufimana, Limnophora.
rusticus, Aëdes.
ruwenzori, Aëdes (*Stegomyia*).
Ryania speciosa, toxicity of extracts of, to mosquitos, **403–410.**
Ryanodine, **404, 409.**

S.

sacharovi, Anopheles.
Sahlbergella singularis, bionomics of, in Gold Coast, **723–744.**
sahlbergellae, Euphorus.
Saissetia catori, **96, 97, 98.**
Saissetia coffeae, **96, 98, 105.**
Saissetia nigra, **96, 97, 98, 105, 106, 114.**
Saissetia oleae, **97, 98, 105, 265.**
Saissetia zanzibarensis, studies on association of *Oecophylla longinoda* with, **93, 96–98, 103–106, 113–134.**
saliceti, Aphis (see *A. farinosa*).
salicti, Chaitophorus (*Pseudomicrella*).
Sambucus canadensis, *Xyleborus morstatti* on, **708.**
Sappaphis plantaginea, **635.**
Sardinia, mosquitos of, **437–494.**
scalaris, Apomecyna.
Schistocerca gregaria, effect of food on growth of, **539–551;** pick-up of spray droplets by flying, **177–197.**
schoutedeni, Helopeltis.
Schradan (Octamethyl Pyrophosphoramide), **59, 686.**
scintillans, Pyrellia.
scitula, Eublemma.
Scolopendra subspinipes subspinipes, **44.**
scottiana, Oligotoma.
Scydmaenus regularis, **44.**
scymni, Centistes.
Scymnophagus, *Xenocrepis* distinct from, **265.**
Scymnophagus mesnili, sp.n., **246, 264–266, 272, 273.**
Scymnophagus secundus, **265.**
Scymnophagus townsendi, *S. mesnili* compared with, **265.**
Scymnus, *Scymnophagus secundus* parasitic on, **265.**
Scymnus abietis, **248, 251.**
Scymnus syriacus, **635.**
secundus, Scymnophagus.
segetum, Agrotis.
seleniticus, Lasiopticus.
senegalensis, Apomecyna (see *A. binubila*); *Hyperaspis.*
sennaarensis, Euponera.
septempunctata, Coccinella.
serena, Dichaetomyia.
sericeum, Melittomma.
serrifera, Dixa.
sexannulatus, Cryptus.
sexpunctatus, Ptinus.
sexpustulatus, Carpophilus.
seychellarum, Icerya.
Seychelles, ants and mealybugs in, **708;** *Melittomma insulare* in, **1–66;** *Xyleborus morstatti* in, **707–710.**
seydeli, Anopheles.
Shell Diesoline, **83, 591, 606, 615, 745.**
Shell Furnace Oil, **89.**
Shell Power Kerosene, **83, 89, 591, 606, 615, 745.**
Shell S.A.E. 20, **89.**
Sierra Leone, incidence of trypanosomes in *Glossina palpalis* in, **797–801.**
Silvestrina, **772.**
simici, Aëdes.
simpsoni, Aëdes (*Stegomyia*).
Simulium neavei, control of *Onchocerca volvulus* by eradication of, in Kenya, **175–176.**
sinaiticus, Culex.
singularis, Sahlbergella.
sitiens, Culex; Stomoxys.
Sitotroga cerealella, **305, 641, 643, 644.**
Skusea (see *Aëdes*).
Sleeping Sickness, *Glossina palpalis fuscipes* transmitting, in Sudan, **790.**
smaragdina, Morellia; Oecophylla.
Snapdragon, *Sappaphis plantaginea* on, **635.**
Soapstone, **305–308.**
Sodium Fluoroacetate, **686, 688.**
Solanum melongena (see Egg-plant).
Sonneratia caseolaris (see Mangrove).
sorbens, Musca (*Byomyia*).
Spalangia drosophilae, factors concerned in host-finding by, **527–537.**
Sphaerocrema striatula (see *Crematogaster*).
spinigera, Lyperosia.
spinthera, Pyrellia.
splendida, Orthellia.
Spray Droplets, pick-up of, by flying locusts, **177–197.**
squamosus, Anopheles.
stampari, Aëdes.
Steatococcus, **98.**
steeleae, Atherigona.
Stegomyia (see *Aëdes*).
stegomyina, Aëdes pulchritarsis.
stellifera, Vinsonia.
Stenobracon deesae, bionomics and rearing of, **647–659.**
Stephanitis pyri (*piri*), **634, 770.**
Stevensonia borsigiana, *Melittomma insulare* on, **27.**
sticticalis, Loxostege.
Stictococcus anonae, **96, 98.**
stigma, Hemerobius.

Stomoxys brunnipes, **789.**
Stomoxys calcitrans, **789.**
Stomoxys nigra, **790.**
Stomoxys sitiens, **790.**
Stomoxys taeniata, **790.**
Stomoxys varipes, **790.**
striatula, Crematogaster (*Sphaerocrema*).
striatus, Figulus.
submaculata, Dixa.
subochrea, Culiseta.
subpilosus, Ptinus.
subspinipes, Scolopendra.
subtilis, Microcerotermes.
succicus, Carpophilus.
Sudan, Anglo-Egyptian, *Apomecyna binubila* in, **553–561;** Muscids of medical interest in, **783–796;** cattle trypanosomiasis in, **784, 785.**
Sumatra (see Indonesia).
sundaicus, Anopheles.
superpictus, Anopheles.
superstitiosus, Dysdercus.
surinamensis, Leucophaea; Oryzaephilus.
suturalis, Fannia.
Switzerland, *Pullus impexus* and *Adelges piceae* in, **243–278.**
swynnertoni, Glossina.
Syria, *Eurygaster integriceps* in, **495–500.**
syriacus, Retithrips; Scymnus.
Syrphus arcuatus, **245, 246, 271, 274.**
Systox, tests of, against insect pests, **59, 683–692, 693–702;** active ingredients of, **683.**
Sytam, **59.**

T.

tachinoides, Glossina.
taeniata, Stomoxys.
Taeniorhynchus (see *Mansonia*).
taeniorhynchus, Aëdes.
Tanganyika Territory, Anophelines in, **361–373, 375–387;** *Glossina* spp. in, **411–421, 585, 605, 613;** new Mirid on cashew in, **703;** *Oecophylla longinoda* in, **94, 98;** Coreid known as *Theraptus* in, **433–435.**
Tannia (see *Xanthosoma sagittifolium*).
Tapinoma melancephalum, **107.**
tarsatorius, Diplazon.
tarsatus, Paltothyreus.
Tarsi (of flies), anatomy of, in relation to insecticides, **711–722.**
Technomyrmex detorquens, **708.**
tectus, Ptinus.
Teepol, **685.**
Temperature, effects of, on action of insecticides, **137–139.** (See Cold-hardiness).
tempestatum, Musca (*Biomyia*).
tempestiva, Musca (*Biomyia*).
Tenebroides mauritanicus, **305.**
tenebrosus, Anopheles coustani.
taerraenovae, Phormia (*Protophormia*).
tessellatus, Eucalymnatus.
Tetrastichus coccinellae, **246.**
textor, Oecophylla longinoda.
Thea bisoctonotata, **635.**
theileri, Culex.
Theobroma cacao (see Cacao).
theobroma, Distantiella.
Theraptus (Coreid known as), bionomics of, **107–109, 429–432;** cross-breeding of strains of, **433–435.**
thirouxi, Lyperosia.
thompsoni, Aphidoletes.
thoracicus, Triaspis.
Thyridanthrax, **168.**
Tineola bisselliella, **579.**
townsendi, Scymnophagus.
Toxaphene, **419.**
Toxoptera aurantii, **98, 104, 635, 772, 773, 777–780.**
translucida, Limnophora.
trapezia, Atherigona.
Triaspis thoracicus, **531.**
Tribolium castaneum, **137–139, 305.**
Tribolium confusum, **641, 642, 643.**
Trichoderma, **120, 121.**
Triethanolamine Oleate, **413.**
trifaria, Ochromusca.
Trinidad, new Cecidomyid parasite of Aphids in, **771, 772, 773, 777–781.**
Triphleps, **246.**
Tripteroides caledonica, **286, 287, 291, 292.**
tristis, Dimorphia.
Trypanosoma, **503, 504.**
Trypanosoma congolense, **798–801.**
Trypanosoma vivax, **797–800.**
Trypanosomiasis, in cattle, **415, 600, 784, 785;** in man, **790.**
Tsetse Flies (see *Glossina*).
turca, Mythimna.
turcicus, Laemophloeus.
Turnip, used in experiments with systemic insecticide, **693–702.**
Typhlops braminus, **44.**

U.

Uganda, mosquitos in, **199–242;** *Oecophylla longinoda* in, **94.**
unguiculata, Uranotaenia.
uniformis, Mansonia (*Taeniorhynchus, Mansonioides*).
United States of America, *Aëdes taeniorhynchus* in, **757–768.**
univittatus, Culex.
Uranotaenia, **207, 438.**
Uranotaenia unguiculata, **444, 445, 458.**

V.

varipes, Stomoxys.
Vegetable Marrow, *Apomecyna binubila* on, **560.**
ventralis, Chrysopa.
verbasci, Anthrenus.
vexans, Aëdes (*Aëdimorphus*).
Vicia faba (see Broad Beans).
vicina, Musca domestica.
viduatus, Aspongopus.
vigilax, Aëdes (*Ochlerotatus*).
Vinsonia stellifera, **105.**
viridis, Coccus.
visci, Carulaspis.
vitripennis, Musca.
vittatus, Aëdes.
vivax, Plasmodium; Trypanosoma.
Volucella zonaria, **580.**
volvulus, Onchocerca.

W.

wahlbergi, Chilocorus.
Walnut, pests of, in Israel, **635.**
Watermelon, *Apomecyna binubila* on, **557, 559.**
watersi, Diparopsis.
Wheat, *Eurygaster integriceps* on, **495, 497, 498, 499.**
Wheat, Stored, used for rearing *Laemophloeus minutus*, **341–350**; *Carpophilus* spp. in, **400, 401**; fumigation of, **639–646.**
wroughtoni, Cardiocondyla.
Wuchereria bancrofti, **423, 425.**

X.

xanthomelas, Musca (*Eumusca*).
Xanthosoma sagittifolium, Pentalonia nigronervosa on, **777.**
Xenocrepis, status of, **265.**
Xenocrepis mexicana, probably referable to *Scymnophagus*, **265.**
Xenocrepis pura, type of genus, **265.**
Xiphistes, **97, 104.**
Xyleborus, **25.**
Xyleborus confusus, **26, 43.**
Xyleborus morstatti, bionomics of, in Seychelles, **707–710**; distribution of, **708.**
Xyleborus perforans, **43.**
Xylena fumosa, cold-hardiness of larvae of, **335.**

Y.

Yellow Fever, **200–203, 207, 232, 233.**

Z.

Zanzibar Protectorate, ants and Coccids in, **93–112, 113–134**; Coreid known as *Theraptus* in, **429–432, 433–435.**
zanzibarensis, Saissetia.
Zenillia caesar, **531.**
ziemanni, Anopheles coustani.
zonaria, Volucella.
zonellus, Chilo.

INDEX TO NAMES OF PERSONS.

Abdel Hai, Ahmed, **793.**
Abdullah Hussein, **793.**
Ahmed Abdel Hai, **793.**
Aitken, T. H. G., **437.**
Alken, R., **621.**
Anstey, D. G., **585.**
Aoki, K., **329.**
Arnold, A. J., **320.**
Asahina, E., **329.**
Avidov (Klein), Z., **637.**

Bagster Wilson, D., **371, 386.**
Baillie, A. F. H., **661.**
Banks, C. J., **751.**
Barnes, H. F., **769, 781.**
Baudi, F., **251.**
Beier, **252.**
Bellamy, L. J., **683, 692.**
Berghe, L. Van den, **501.**
Blackith, R. E., **645.**
Blake, F. W., **786, 793.**
Blake, Mrs. G. M., **575, 582.**
Bloss, J. F. E., **793.**
Bodenheimer, F. S., **637.**
Booker, W. L., **801.**
Bovey, P., **275.**
Brown, A. W. A., **67, 525.**
Brown, E. S., **1, 429** (note), **707.**
Browning, E., **63.**
Bugher, J. C., **232.**
Burnett, G. F., **411, 602, 605, 613.**
Bushe, W., **793.**
Butler, M. C. F., **386.**
Buxton, P. A., **793.**

Capra, F., **251.**
Caresche, L., **63.**
Carne, R., **705.**
Charles, L. J., **403.**
Chaudhuri, R. P., **647.**
Choyce, M. A., **680.**
Church, B. M., **756.**
Coppel, H. C., **276.**
Cormack, I., **310.**
Cottam, R., **793.**
Cotton, **63.**
Coutts, H. H., **749.**
Crawford, F., **63.**
Crawford, J. H., **613, 614, 615.**

Dade, H. A., **709.**
D'Aguilar, J., **252.**
Darling, R. C. Maxwell-, **793.**
Dauber, G. C., **92, 602, 749.**
Davey, P. M., **539.**
David, W. A. L., **683, 693.**
Davies, D. E., **550.**
Davies, D. M., **78.**
Davies, R. G., **349, 358, 402.**
Delcellier, H. A., **77.**
Delucchi, V., **243.**
Dirsh, V. M., **63.**
Dobson, R. M., **389.**
Doncaster, J. P., **637.**
Dookley, J., **63, 709.**
Dowson, W. J., **63.**
Duffy, E. A. J., **63, 709.**
Dun, G. S., **703.**
Durocher Yvon, F., **63.**
du Toit, R., **600.**

Eastop, V. F., **771.**
Elliott, M., **320.**
Ellis, M. B., **709.**
Emden, F. I. van, **63, 793.**

Felt, E. P., **769.**
Ferrière, C., **264, 267, 276.**
Fiedler, O. G. H., **600.**
Fisher, L. M., **78.**
FitzGerald, D. Vesey-, **2, 63.**
Foote, R. H., **769.**
Fox Wilson, G., **771.**
Franz, J., **251, 255, 256, 257, 265, 272, 273, 276.**
Freeman, J. A., **349, 358, 402.**

Gagliardi, A., **252.**
Gahan, A. B., **265.**
Gardiner, B. O. C., **683, 693.**
Garnham, P. C. C., **175.**
Geering, Q. A., **661.**
Gillies, M. T., **361, 375.**
Glasgow, J. P., **563.**
Gledhill, J. A., **420, 602.**
Glover, P. E., **174.**
Goodey, T., **320.**
Gracie, W. McAuley, **295.**
Graham, A., **744.**
Greer, E. N., **349.**
Gunn, D. L., **196, 550.**

Haddow, A. J., **199.**
Haeger, J. S., **757.**

Hall, W. J., **63, 110, 132, 432.**
Hammond, J. H., **583.**
Harpaz, I., **637.**
Harris, W. V., **63.**
Haufe, W. O., **507.**
Heath, D. F., **683.**
Hille Ris Lambers, D., **635, 637.**
Himid, Said, **110.**
Hincks, W. D., **63.**
Hinton, H. E., **390, 402.**
Hinz, R., **276.**
Hocking, K. S., **92, 420, 585, 605, 613, 749.**
Hunter-Jones, P., **550.**
Hussein, Abdullah, **793.**

Ingham, F., **78.**

Jackson, C. H. N., **413, 420, 602.**
James, Mrs. J., **110.**
Johnson, C. G., **756.**
Jones, A. C., **77.**
Jones, G. E., **500.**
Jones, P. Hunter-, **550.**
Jursic, F., **525.**

Kerr, R. W., **313, 317, 323.**
Kerridge, J., **316, 328.**
King, H. H., **793.**
Kirkpatrick, T. W., **771, 772, 774, 777.**
Klein (see Avidov).
Kluge, E. B., **600.**
Kockum, S., **295.**
Krause, G., **256.**

Laing, G. L., **310.**
Laird, M., **279, 285, 423.**
Lambers, D. Hille Ris, **635, 637.**
Lambrecht, F. L., **501.**
Le Pelley, R., **295.**
Lewis, C. T., **711.**
Lewis, D. J., **783.**
Lieftinck, M. A., **426.**
Lord, K. A., **328.**
Lovemore, D., **602.**
Lumsden, W. H. R., **203, 208.**

McAuley Gracie, W., **295.**
Macfarlane, Mrs. M., **139.**
McIntosh, A. H., **137.**
McMahon, J. P., **175.**
Maqsud Nasir, M., **639.**
Marshall, Sir G., **63.**
Marshall, L. A., **320.**
Marthaler, A., **276.**
Martin, Hubert, **526.**
Matenga, Teariki, **426.**
Mattingly, P. F., **489.**
Maxwell-Darling, R. C., **561, 793.**
Menzel, **271.**
Mesmer, E. T., **92, 611, 749.**
Mesnil, L. P., **247, 264, 275.**
Middleton, W. E. K., **77.**
Miles, H. W., **402.**
Miller, N. C. E., **703.**
Mohammed Shaar, **793.**
Moran, T., **349.**
Morris, H. J., **793.**
Munro, J. W., **349, 358, 645, 722.**

Narayanan, E. S., **647.**
Nasir, M. Maqsud, **639.**
Needham, P. H., **316, 320.**
Nelder, J. A., **756.**
Newton, H. V., **611.**
Nielsen, E. T., **757.**
Nijveldt, W., **770.**
Nixon, G. E. J., **63, 132.**
Norris, M., **550.**
Nutman, F. J., **110, 132.**

Ogg, Sir W. G., **328.**
Ojjiki, F. J., **386.**
Osumbah, A. J., **386.**

Page, A. B. P., **645, 722.**
Parker, H. W., **63.**
Parsons, B. T., **163.**
Pearson, E. O., **662, 680.**
Pelley, R. Le, **295.**
Pereira, H. C., **310.**
Pollard, D. G., **553.**
Pope, C. P., **756.**
Pope, R. D., **63, 709.**
Potter, C., **320, 328.**
Provost, M. W., **761.**

Ramell, L. G., **583.**
Ramsdale, C. D., **386.**
Richards, O. W., **349, 358, 402.**
Ris Lambers, D. Hille, **635, 637.**
Robertson, P. L., **135.**
Robinson, J., **92, 420, 749.**
Robinson, P., **296, 310.**
Ross, E. S., **63.**
Rungs, C., **252.**
Ruttledge, W., **793.**

Sachtleben, H., **770, 771.**
Said Himid, **110.**
Sawyer, K. F., **177.**
Sell, R. C., **420, 605, 613.**
Shaar, Mohammed, **793.**
Shinozaki, J., **329.**
Simmonds, F. J., **2, 63, 527.**
Smallman, B. N., **526.**

Smit, A. N., **574.**
Smith, R. G., **310.**
Solari, F., **251, 252.**
Southgate, B. J., **575.**
Speyer, W., **770, 771.**
Squire, F. A., **797.**
Steele, M., **793.**
Stevenson, A. C., **282.**
Strickland, A. H., **744.**
Swain, R. C., **310.**
Swaine, G., **703, 704.**
Swirski, E., **623.**

Tait, E. M., **429, 433.**
Talhouk, A. S., **495.**
Tattersfield, F., **316, 323, 328.**
Taylor, Mrs. L. R., **316.**
Taylor, T. H. C., **550.**
Thompson, B. W., **79, 621.**
Thompson, W. R., **275.**
Toit, R. du, **600.**
Tomsett, J. E., **550.**
Townsend, J., **110.**
Trapido, H., **438.**
Trew, J. K. M., **793.**
Twinn, C. R., **78.**

Uvarov, B. P., **550.**

Van den Berghe, L., **501.**
Vanderplank, F. L., **432, 435.**
van Emden, F. I., **63, 793.**
Vesey-FitzGerald, D., **2, 63.**
Voelcker, O. J., **726.**

Watson, D. L., **78.**
Watters, **709.**
Way, M. J., **93, 113.**
Weitz, B., **372.**
Wertheim, G., **637.**
Whiteside, E. F., **420.**
Wichmann, H. E., **246, 255, 259, 260.**
Wigglesworth, V. B., **338.**
Williams, C. B., **240.**
Williams, D. J., **110.**
Williams, D. W., **402.**
Williams, G., **723.**
Williams, G. C., **341, 351.**
Wilson, C. E., **793.**
Wilson, D. Bagster, **371, 386.**
Wilson, D. H., **320.**
Wilson, F., **574.**
Wilson, G. Fox, **771.**
Wilson, S. G., **141, 174.**
Wiltshire, S. P., **63, 708.**
Woodroffe, G. E., **135, 575.**
Wootten, N. W., **177.**
Wylie, H. G., **251.**

Yasumatsu, K., **637.**
Yeo, D., **79, 585, 611, 621, 745.**
Yvon, **292.**
Yvon, F. Durocher, **63.**

Zimmerman, E. C., **425.**
Znatowicz, S., **420, 602, 611, 621.**

1/1 PB